POPULATION ECOLOGY OF MYZUS PERSICAE (SULZER)

by

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ABSTRACT

Most of the work described in this thesis was done with the apterous form of Myzus persicae (Sulzer). Different body parts of the 4 nymphal instars and the adult apterae reared at certain constant temperatures (15°C, 25°C and 28°C) were measured. Methods suitable for distinguishing the various instars are described and discussed.

The effects of constant temperatures (10°C, 15°C, 20°C, 25°C and 29°C) and of two host plants (potatoes and brussels sprouts) on experimental populations of M. persicae were assessed by calculating the intrinsic rates of increase.

The effects of critically high and low temperatures on development, size and fecundity were examined and a study made of the ability of aphids to recover when returned to a suitable temperature.

Field populations of aphids on potatoes were assessed in 1967 and 1968. Actual and intrinsic rates of increase were calculated. The possible influence of the main biotic and abiotic factors on the population fluctuations were examined and discussed. Experiments were also made using potatoes and brussels sprouts to investigate the effects of different natural enemies and of rainfall on M. persicae populations using exclusion technique and an insecticidal check method.

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SECTION I. MORPHOLOGICAL STUDIES ON THE DIFFERENT INSTARS OF MYZUS PERSICAE (SULZER).

A. INTRODUCTION.

The recent approach to the study of aphid populations through instar distribution necessitated the knowledge of reasonable means of differentiating aphid populations into their various stages. Relevant research on Myzus persicae is sparse and the results presented by the pioneer workers - Soliman (1951) and Sylvester (1954) are somewhat contradictory. Ôtake (1958, 1966) and the above two workers used the lengths of the antennal segments as criteria for distinguishing Myzus persicae instars, but encountered some difficulties. Kershaw (1964), however, tried a different method which depended on the differential densities of the instars. His observations showed that the rates of fall in a suspension of the fourth, third, second and first instar were progressively slower (by 1.1, 1.5, 2.7 and 4.3 times respectively) than that of adult aptera.

The present work followed the same lines as Soliman's and Sylvester's, but aimed at a more reliable means of distinguishing between the various instars and at clarifying points of controversy.

B. MATERIALS AND METHODS.

(1) Stock culture.

A culture of M. persicae on brussels sprouts was started in October, 1966 in a room at a constant temperature of 20°C,

illuminated for 16/24 hours. The individuals which formed the nucleus of this culture originated from a single apterous viviparous mother. Aphids from this culture were used for the various experiments.

(2) Techniques for obtaining successive instars.

A preliminary trial was carried out in a room at a constant temperature of 25°C illuminated for 16/24 hours. Pairs of 9 cm petri-dishes were used to enclose moist filter papers bearing leaves of brussels sprouts. Adult apterae were transferred to each petri-dish and allowed to reproduce for six hours after which they were removed and about 10 progeny left in each dish. Observations were made twice a day and any exuviae were recorded and removed. The leaves were replaced with fresh ones every day and aphids were transferred by gently disturbing each until it withdrew its stylets, when it was directed to the fresh leaf.

Later experiments were done at 15°C, 25°C and 28°C constant temperature rooms with 16/24 illumination. The above technique required too frequent disturbance of the aphid and also occupied much space. Johnson and Birk's (1960) method as modified by Hughes and Woolcock (1965) was therefore used in all other experiments. The aphids were kept on leaf-discs floating on a dilute culture solution and in these conditions they remained at least a week without deteriorating. Groups of 2" x 1" specimen tubes filled with $1\frac{3}{4}$" of culture solution were each put in a plastic box. 10 boxes containing 150 sample tubes were arranged in controlled environment rooms at 15, 25 and 28°C, illuminated for 16/24 hours. Leaves of

brussels sprouts were obtained from the field and $\frac{5}{8}$" diameter leaf-discs were cut as described by Hughes and Woolcock (1965) and floated on the solutions. 2 - 3 adult apterae were transferred with a camel brush to each leaf-disc. After 3 hours the adults were removed and single nymphs were left on each leaf-disc. The nymphs removed were kept as examples of the first instar. The whole set-up was covered with glass sheets to prevent exuviae from being blown away. Observations continued twice a day and about 25 individuals of each instar were removed for measuring. The leaf-discs remained healthy and unchanged for the duration of the experiment. The level of the culture solution in the sample tubes was maintained by adding fresh solution when required.

(3) Preparation and mounting.

Individuals of the same stage were transferred to a test tube with 90% alcohol and heated on a boiling water bath for about 5 minutes. The alcohol was then decanted and replaced with 10% KOH and the contents were transferred to a boiling water bath for about two minutes. The KOH was then decanted and aphids washed in 3 changes of 90% alcohol; chloralphenol (chloral hydrate + phenol crystals) was then added and the contents heated for about 25 minutes. The aphids were then mounted in gum chloral medium. The slides were left over for some hours for the medium to get slightly hard before applying the cover-slip. This minimised body distortion from compression by the cover-slip. Measurements of the various parts was made by using a micrometer eyepiece mounted on a high power binocular microscope

at a magnification of x10. The length of the aphid was measured from the vertex to the extreme end of the cauda; and the width at the widest portion of the insect. The lengths of the antennal segments, cauda, cornicle, rostrum and hind tibia and tarsus were also measured. Groups of 10 - 20 individuals of each instar were measured at each temperature.

C. RESULTS.

Anatomical measuremetns of the various parts with their standard errors are presented in tables 1 (petri-dish expt.) and 2 (25°C), table 3 (15°C) and table 4 (28°C).

All the parts measured under the different temperature levels grew with each successive instar, except for the rostrum which measured the same in the first and second instars; also the third antennal segment in the third instar was shorter than in the second, being segmented to give the fourth segment. The lengths of the rostrum, hind tarsus and 1st and 2nd antennal segments did not alter significantly ($P = > 0.05$) between any two successive instars and their length limits overlapped. These characters are, therefore, unsuitable for distinguishing the different instars.

The data from the different temperature regimes show that the sizes of most of the parts measured were inversely related to temperature. Thus the mean lengths and widths of the first and second nymphal instars were always smaller when reared at 15°C than at 25°C, while at 15°C the same parts for the third and fourth instars and adult apterae exceeded those of the individuals reared at 25°C.

Table 1. Measurements (microns) of the four nymphal instars and adult Myzus persicae (Sulzer) reared at 25°C - Petri-dish technique..

	Instar				Adult
	First	Second	Third	Fourth	
Body length	757.4 ±16.2	845.2±30.7	1046.6±23.2	1280.6±20.9	1803.6±58.0
Body width	401.7±4.0	461.7±8.7	592.2±10.4	660.9±11.0	966.7±41.8
Antennal segment I	53.2±1.2	56.5±1.7	67.8±1.2	73.9±1.2	87.6±1.7
Antennal segment II	47.5±1.2	48.5±1.2	58.3±1.2	66.9±1.2	74.1±1.7
Antennal segment III	110.8±1.7	155.0±12.7	148.6±2.9	239.6±2.9	430.0±10.4
Antennal segment IV			147.1±0.6	200.9±2.3	325.4± 15.1
Antennal segment V	81.3±1.7	94.2±4.0	138.0±2.3	167.9±3.5	251.7± 9.3
Base VI	76.2±1.7	78.9±2.3	96.9±1.7	110.8±1.2	134.3±3.5
Unguis	209.1±1.7	243.2±9.8	338.3±6.4	393.9±7.5	444.4±12.2
Total antenna	578.1±5.8	676.4±30.2	995.0±11.6	1254.2±13.9	1747.7±47.6
Cauda	65.4±1.7	79.8±4.0	84.8±5.2	96.5±4.6	211.6±6.9
Cornicle	112.1±0.6	138.1±6.9	224.0±5.2	289.8±4.0	461.7±16.2
Rostrum segments IV+V	83.4±0.6	83.2±0.6	91.9±1.2	98.7±0.6	106.0±32.5
Hind tibia	314.0±4.1	351.7±16.2	506.7±9.9	655.0±8.1	1059.5±32.5
Hind tarsus	83.5±1.2	83.6±1.7	97.6±1.2	107.6±1.2	115.9±2.9

Table 2. Measurments (microns) of the four nymphal instars and adult aptera M. persicae (Sulzer) reared at 25°C - Leaf-disc technique.

	Instar				Adult
	First	Second	Third	Fourth	
Body length	662.8±18.6	854.9±25.5	1017.9±19.1	1392.2±21.5	1731.8±33.6
Body width	377.1±18.6	510.1±14.5	630.7±11.6	861.5±18.0	939.2±23.8
Antennal segment I	45.7±0.6	51.9±1.2	60.8±0.6	70.1±0.6	79.2±0.6
Antennal segment II	42.3±0.6	47.2±1.2	53.9±0.6	62.3±0.6	69.3±1.2
Antennal segment III	93.3±2.2	164.3±3.4	139.2±1.9	243.1±6.4	405.5±9.3
Antennal segment IV			127.6±2.5	180.4±6.5	285.9±7.0
Antennal segment V	68.8±0.5	94.0±2.6	124.7±2.6	155.7±4.6	217.3±7.0
Base VI	62.3±0.5	72.3±1.2	83.0±0.6	98.0±2.5	113.5±2.5
Unguis	204.9±3.0	257.3±7.0	295.6±4.6	350.8±8.1	412.3±10.4
Total antenna	517.3±5.5	687.1±13.7	883.6±5.2	1160.4±27.3	1583.1±32.5
Cauda	32.4±0.6	56.2±3.5	62.6±2.9	99.7±3.5	192.8±4.1
Cornicle	106.5±1.0	158.6±2.4	217.7±2.5	301.9±4.0	454.9±6.9
Rostrum segments IV+V	78.1±1.2	79.7±0.6	85.7±1.2	95.8±1.2	99.6±0.6
Hind tibia	264.9±3.0	358.9±4.6	465.9±4.0	654.9±0.5	1006.1±15.7
Hind tarsus	74.7±1.2	82.1±1.2	86.7±0.6	104.4±1.7	112.9±1.2

Table 3. Measurements (microns) of the four nymphal instars and adult aptera M. persicae (Sulzer) reared at 15°C.

	Instar				Adult
	First	Second	Third	Fourth	
Body length	582.4±18.0	778.8±24.9	1126.8±41.2	1469.8±22.6	1900.9±37.1
Body width	277.1±8.1	375.4±15.1	659.0±37.7	921.2±19.1	1028.0±29.0
Antennal segment I	46.5±1.2	54.6±1.2	66.4±1.7	77.6±1.7	88.2±1.2
Antennal segment II	40.2±0.6	45.5±1.2	55.0±1.2	62.4±1.2	71.0±1.2
Antennal segment III	93.5±1.4	159.4±2.7	141.3±5.9	236.5±4.4	399.2±4.2
Antennal segment IV			139.8±4.1	203.9±3.8	310.5±7.5
Antennal segment V	65.7±1.8	89.7±1.7	132.0±4.6	177.1±2.9	246.5±4.6
Base VI	61.5±1.2	74.1±1.2	95.0±2.3	107.6±1.2	124.9±1.7
Unguis	190.7±2.9	241.4±4.1	319.0±5.8	375.7±4.6	428.2±5.8
Total antenna	498.1±19.7	664.7±8.1	948.7±22.0	1240.9±15.7	1668.5±1.7
Cauda	36.4±2.3	56.5±19.7	70.2±3.5	83.4±2.3	195.8±2.3
Cornicle	104.6±1.6	150.3±2.1	216.7±4.2	299.5±4.5	458.3±8.1
Rostrum segments IV+V	76.6±0.6	79.8±1.2	88.9±1.2	99.4±1.2	101.5±1.2
Hind tibia	262.4±5.8	357.6±5.4	503.6±11.8	674.9±10.6	994.3±13.9
Hind tarsus	73.3±1.2	81.4±1.2	94.6±1.2	107.1±1.2	115.6±1.7

Table 4. Measurements (microns) of the various body parts of the four nymphal instars of M. persicae (Sulzer) reared at 28°C.

	First	Second	Third	Fourth
Antenna				
Segment III	84.6±0.1	148.8±1.8	129.8±2.2	230.3±3.0
" IV			115.9±2.0	174.7±3.1
" V	62.1±0.1	84.8±0.1	113.3±1.3	147.1±1.6
" VI	240.1±2.0	300.3±3.5	359.1±4.9	428.2±4.9
Total	386.8±3.2	533.9±5.5	718.2±9.2	980.2±11.1
Cornicle	88.1±0.1	129.7±1.0	193.3±1.5	276.8±2.0
Hind tibia	234.2±4.4	315.1±4.9	423.3±7.2	610.1±6.1

The antennae was shorter than the body length in all instars and at the two temperature levels tested (15 and 25°C). The lengths of antennal segments III and IV in the third instar were almost similar at 15°C but exhibited significant differences at 25°C and 28°C at $p = < 0.01$ and $p = < 0.001$ respectively (table 5). The lengths of the IVth and Vth segments in the same instar were almost similar at the same temperature, but were negatively correlated with temperature (table 6).

The lengths of the IIIrd and IVth segments in the fourth instar showed significant differences at the three constant temperatures. However, these differences were greater at high temperatures (25 and 28°C), suggesting that the ratio of IIIrd to IVth segments is temperature dependent.

Table 5. Lengths of antennal segments III and IV (microns) in the third and fourth instars reared at three constant temperatures.

	15°C		25°C		28°C	
INSTAR	III	IV	III	IV	III	IV
Third instar	141.3±5.9	139.8±4.1	139.2±1.9	127.6±2.5 **	129.8±2.2	115.9±2.0 ***
Fourth instar	236.5±4.4	203.9±3.8	243.1±6.4	180.4±6.5	230.3±3.0	174.9±3.1

** $p < 0.01$ - *** $p < 0.001$

Table 6. Lengths of antennal segments IV and V (microns) in the third instar.

segment	15°C	25°C	28°C
IV	139.8±4.1	127.6±2.5	115.9±2.0
V	132.0±4.6	124.7±2.6	113.3±1.3

Figs 1 and 2 show the relationship of the length of the IIIrd antennal segment to the total length of parts of the antenna at the three temperatures. (A) shows the distribution for the first and second instars, while (B) shows that for the third and fourth instars. In this context the whole antennal length excluding the Ist and IInd segments will be referred to as the"total"length, while that excluding the Ist, IInd and VIth segments as the "intermediate" length. In fig 1 the IIIrd segment is compared with the "intermediate length of the four nymphal instars; the same segment is compared with the "total"length of the antenna in fig 2.

Fig. 1. Relationship between the length of the third antennal segment and the 'intermediate' segments at three constant temperatures.

Fig. 1.

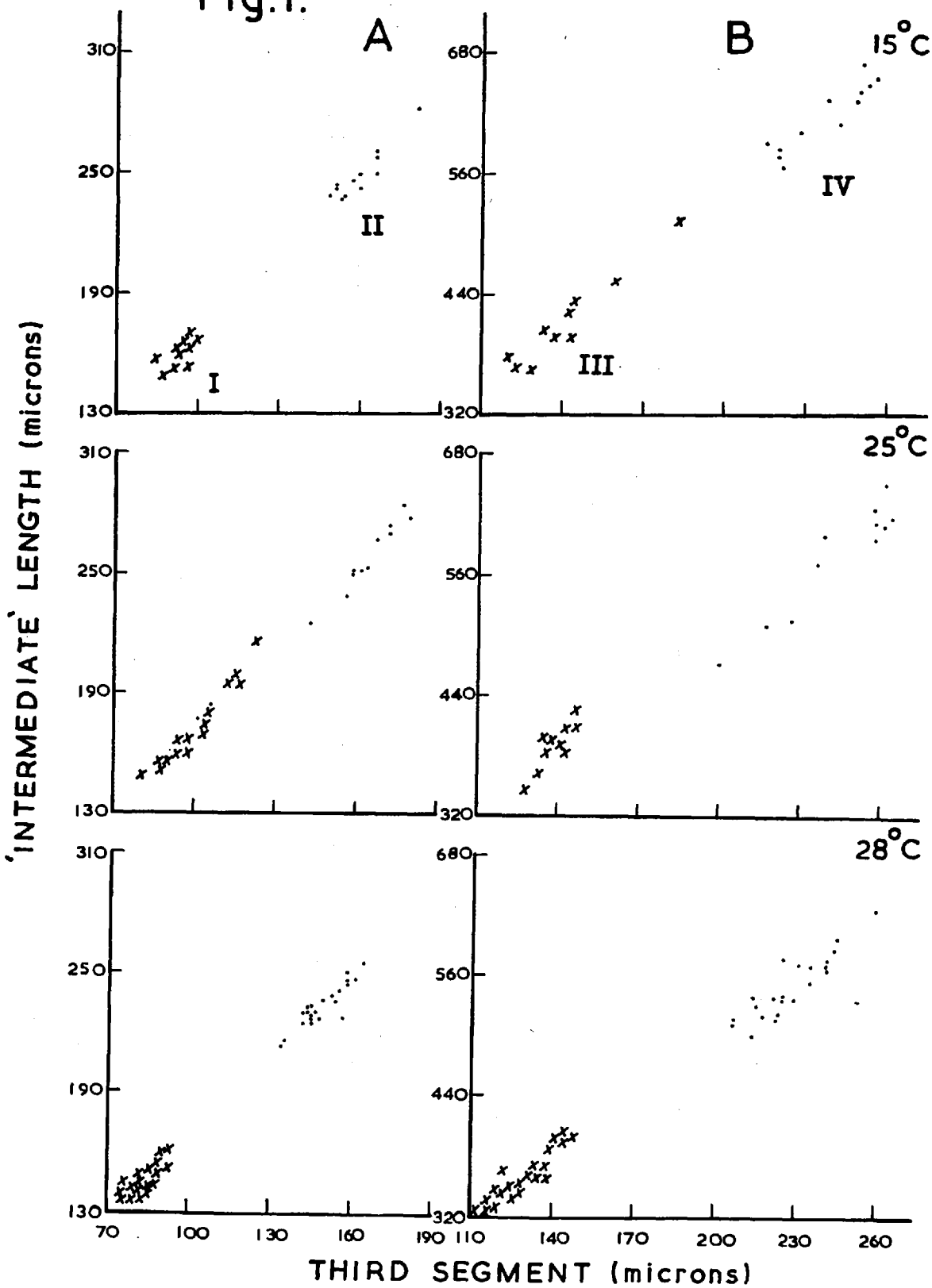
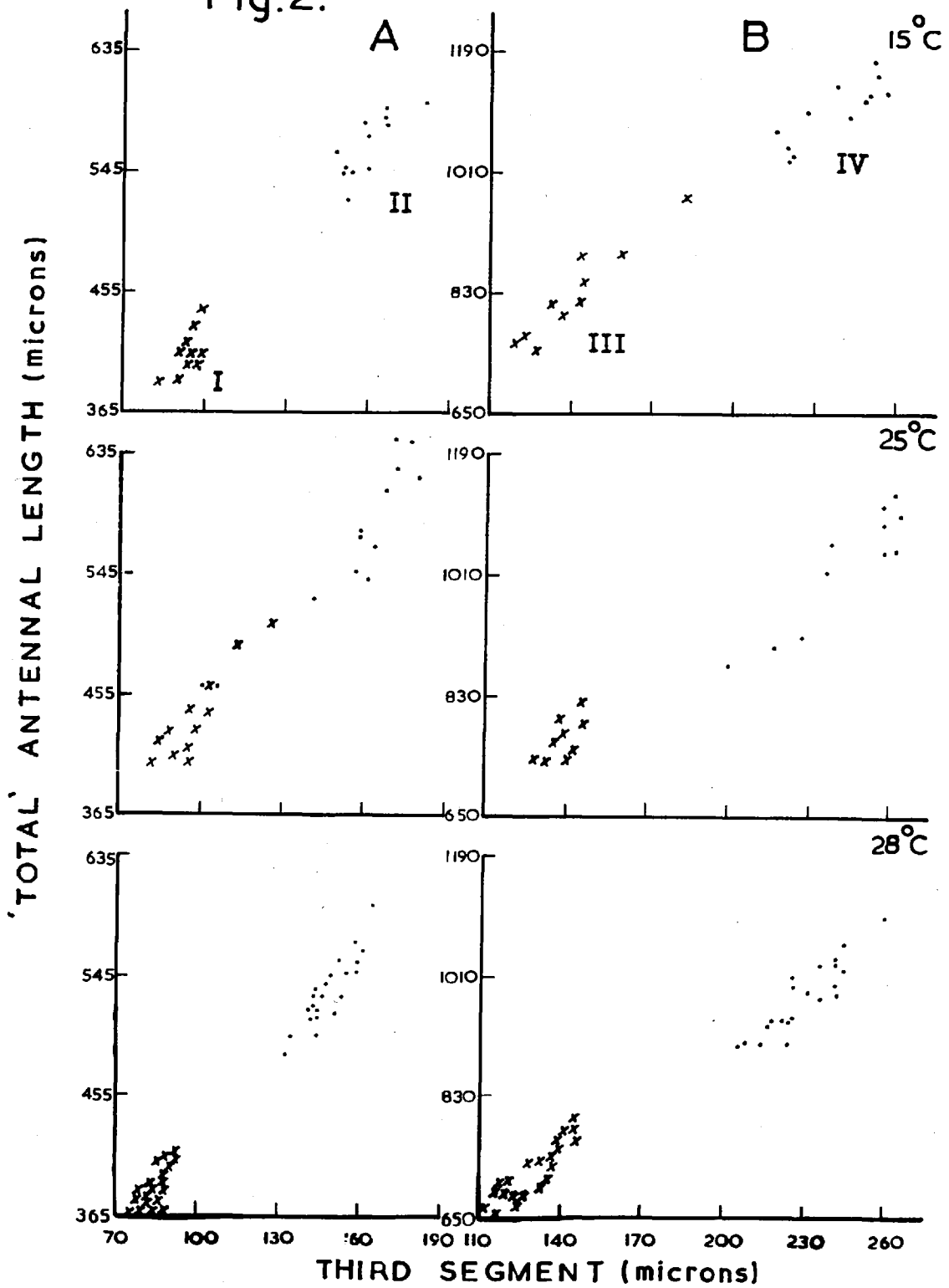

A
B
15°C
25°C
28°C
I
II
III
IV
310
250
190
130
680
560
440
320
70
100
130
160
190
110
140
170
200
230
260
'INTERMEDIATE' LENGTH (microns)
THIRD SEGMENT (microns)

Fig. 2. Relationship between the length of the third antennal segment and the 'total' length at three constant temperatures.

Fig.2.


A
B
15°C
25°C
28°C
I
II
III
IV
635
545
455
365
1190
1010
830
650
70
100
130
160
190
110
140
170
200
230
260
'TOTAL' ANTENNAL LENGTH (microns)
THIRD SEGMENT (microns)

The distribution of the individuals in these figures shows that the length of the IIIrd segment in the first and second instars on one hand and the third and fourth on the other remain distinct at the same temperature, although the difference between the third instar reared at low temperature (15°C) and the fourth instar reared at high temperatures (25 and 28°C) is small. The "total" and "intermediate" lengths of the antennae are also distinct at the same temperature, but their limits vary rather widely in the third instar at 15°C. Thus their antennal lengths overlap that of the fourth instar at 25°C and 28°C. It is also clear that the overlap is greater for the "total" length than for the "intermediate" length, indicating that the length of the VIth segment varies widely.

The length of the cornicle increased steadily from first instar to the adult aptera; the difference between any two successive instars being significant at $p = < 0.001$ level. The maximum and minimum lengths in the four instars are presented in table 7 which shows that no overlapping occurred between the different instars irrespective of temperature.

Table 7. Maximum and minimum lengths (microns) of the cornicle in the various instars.

INSTAR	15°C	25°C	28°C	overall limits
First	97.1-112.4	99.0-110.5	80.9-97.9	80.9-112.4
Second	140.9-165.7	148.6-169.5	119.7-136.8	119.7-169.5
Third	201.9-243.8	209.5-228.6	181.9-209.9	181.9-243.8
Fourth	283.8-331.4	289.5-325.7	258.2-292.4	258.2-325.7

Fig. 3. Hind tibia ratio of the nymphal instars at three constant temperatures.

Fig.3.

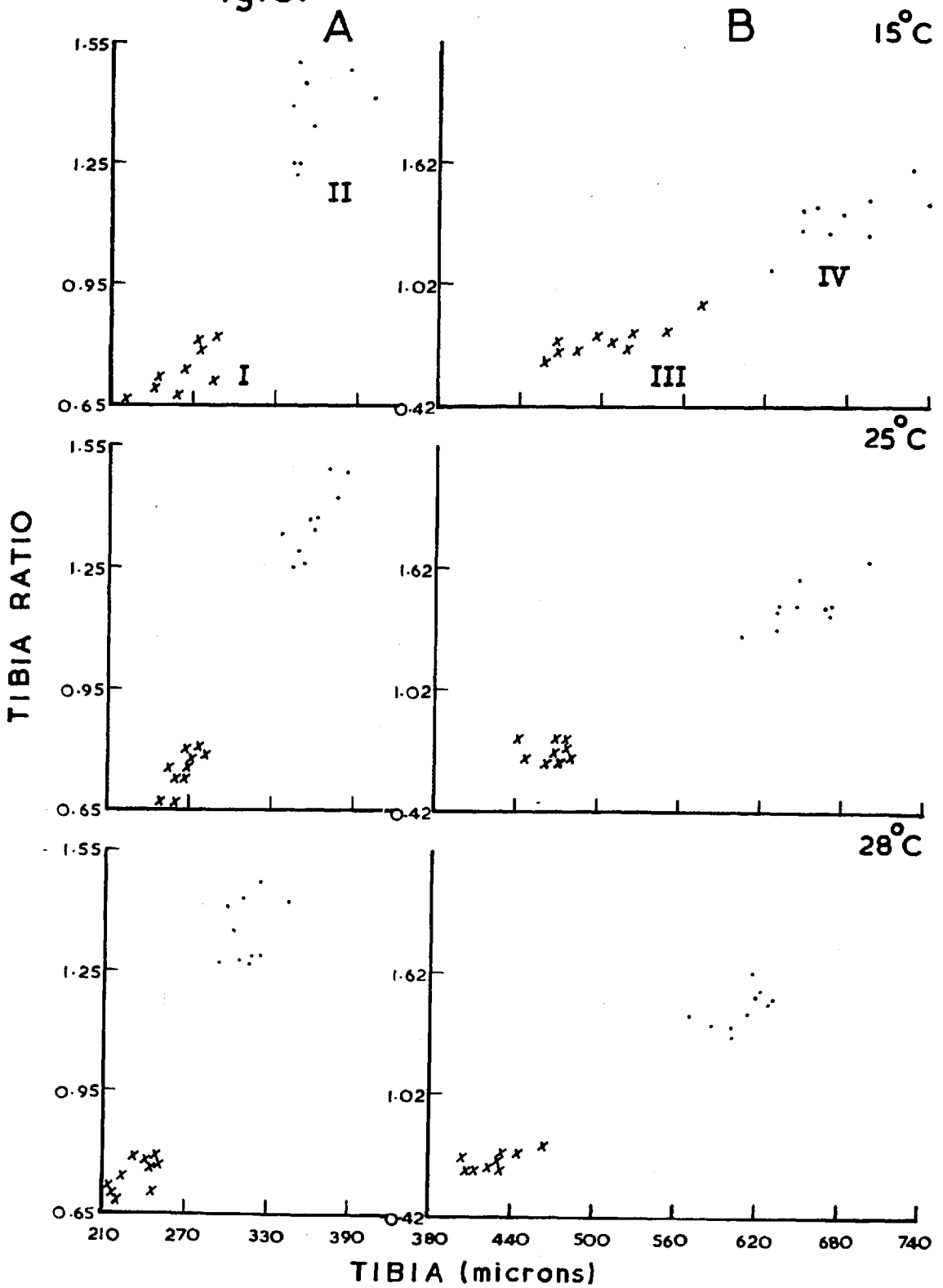

A
B
15°C
25°C
28°C
I
II
III
IV
1.55
1.25
0.95
0.65
1.62
1.02
0.42
TIBIA RATIO
210
270
330
390
380
440
500
560
620
680
740
TIBIA (microns)

Fig.3 shows the length of the hind tibia of the four nymphal instars and the ratios of the first to the second instars (A) and the third to the fourth (B). This part is greatly affected by the temperature and the length of the different instars overlap.

D. DISCUSSION.

During their investigations on instar length in Brevicoryne brassicae (L.) Hughes and Woolcock (1965) kept the insect on leaf-discs on culture solution. Brussels sprouts leaf-discs did not deteriorate for at least a fortnight and thus the danger of damage while handling a very soft insect was minimised. The method is more promising for relatively sessile aphids like B. brassicae than for M. persicae which is an active species and is thus liable to drown or escape. Losses from such causes are most pronounced under unfavourable conditions, e.g. at critical high temperatures, when the aphid is most restless.

The virginopara of M. persicae appear to be morphologically diverse perhaps because of the widespread distribution and polyphagous nature of the species. Many of the results obtained by different workers in different localities seem to contradict. Cartier and Painter (1956) stated that the body size of the nymphs varied markedly with the host plant conditions. Bodenheimer and Swirski (1957) reported that the body size of nymphs was affected by the seasonal conditions; the biggest individuals appeared in the cool season and the smallest in the hot season. It seems that the host plant condition

and the temperature are the most important two factors conditioning the size of the aphid within an instar. The sizes of soft parts of the aphid i.e. the body length and the width are the most sensitive to these two factors and are therefore not suitable for detecting the various instars (table 8 and 9). Instead the less sensitive chitinous segments have been most studied (Ôtake, 1966).

Table 8. Range of the body length (microns) at 15 and 25°C.

Temp.	INSTAR			
	First	Second	Third	Fourth
15°C	524-712	657-916	905-1390	1352-1587
25°C	571-743	712-977	933-1161	1257-1486

Table 9. Range of the body width (microns) at 15 and 25°C.

Temp.	INSTAR			
	First	Second	Third	Fourth
15°C	249-328	350-516	451-838	773-998
25°C	286-448	438-594	581-705	756-937

Soliman (1951) investigated some of the morphological characters of the various instars by rearing the aphid in cages on potato leaves, Sylvester (1954) reared them on leaf-discs of mustard, Brassica juncea at average temperatures 24°C and 23.2°C. His results contradicted Soliman's in many ways. Thus the length of the antenna, stated by Soliman to be longer than the body length in the first, third and

fourth instars was found by Sylvester and by myself to be shorter than the body length in all instars (tables 1, 2 and 3). Soliman also found that the IVth antennal segment was longer than the IIIrd in the third nymphal instar, but Sylvester and myself have found them to be equal or the IIIrd slightly longer than the IVth, never vice-versa in any instar (table 5). Soliman, also stated that in the adult aptera segment III and IV were of equal length, while the present results indicated a longer segment III. Thus the present results confirm many of the findings of Sylvester. The latter refers this controversy to the fact that Soliman used diaphane, a mounting medium which causes the soft parts of the body to shrink, but the present author thinks that the mounting medium or techniques of preparation affected more the antenna, since it is this part on which most of the differences centre. Variability of antennal segments is also reported by Harpaz (1953) who stated that IIIrd, IVth and Vth segments were more variable than all other parts of Rhopalosiphum maidis.

Sylvester's method of taking the antenna as criteria to detect the various instars is accepted as being of practical value especially where appreciable handling of the specimen is to be avoided. However, the length of the antenna, in relation to the body length which he used to differentiate between the first and second instars varies widely and in many cases there is overlap at the same constant temperature (table 10).

Table 10. Range of length in microns of the first and second instar antennae at 25°C relative to body length.

INSTAR	
First	Second
0.687-0.875	0.735-0.890

The suggested equal mean lengths of segment III and IV in the third instar was his criteria for distinguishing between the third and fourth instars since in the latter the length of the IIIrd segment exceeded that of the IVth segment. But measurements made in the present work show that there is a significant difference between segments III and IV in the third instar at 25°C and 28°C, although they are almost equal at 15°C (table 5). The levels of significance being at $p = < 0.01$ and $p = < 0.001$ at 25 and 28°C respectively. However, the IVth and Vth segments are almost equal in length at all three temperatures (table 6), although inversely affected by temperature. Therefore the evidence that the IVth and Vth segments are equal in the third instar, but not in the 4th instar is more reliable than Sylvester's data on the IIIrd and IVth segments. It can be concluded that Sylvester's method is a practical one although there will be some error in differentiating the first and second instars; also it seems that the relative lengths of the IVth and Vth segments of the antenna is more reliable for differentiating the third and fourth instars than Sylvesters's distinction using the IIIrd and IVth segments.

The antenna although variable has been used in most of the work on 'classifying'instars. Otake (1966) used the relationship between IIIrd and the "intermediate" lengths of the antenna but found out that it was difficult to differentiate the third and fourth instars. The present results indicate that it is as well difficult to differentiate the first and second instars on the same basis as these lengths overlap (fig. 1).

The hind tibia (fig. 3) is also variable at different temperatures and the possibility of using the absolute length to distinguish between the different instars is open to error.

Another method which is believed to give better results is here suggested for conditions where individuals can be mounted and measured i.e. where the specimen is not needed alive. The length of the cornicle in the different instars differs in successive instars. The maximum and minimum measurements and the overall limits presented in table 7 indicate that no overlapping occurred irrespective of temperature. It could be concluded that the cornicle length is a simple part to measure and will give a sound means of detecting the different instars. Eastop (unpublished results) has also used the length of the cornicle in relation to the ultimate rostral segment to differentiate the first and second instars and also the cornicle in relation to antennal segment III to differentiate between the third and fourth instars. This confirms that in any particular instar the cornicle probably varies less in length than do other segments of the body.

SECTION II. EFFECT OF TEMPERATURE ON THE EXPERIMENTAL POPULATION OF MYZUS PERSICAE (SULZER).

A. INTRODUCTION.

Barlow (1962) studied the effect of temperature on the experimental populations of M. persicae and Macrosiphum euphorbiae (Thomas) and reported that the former was a species with a high potential for increase. However, in nature the free progress of the population is checked by a number of complex biotic and abiotic factors which keep it low (Vevai, 1942; Broadbent and Hollings, 1951; Otake, 1961; Ramaseshiah, 1967; Tamaki et al, 1967 and Mackauer, 1968). In laboratory studies on the population of the aphid, most of the biotic and abiotic factors can be eliminated, and the effect of the temperature, which is the major climatic factor regulating the rate of growth of the population can be tested.

Temperature regulates the growth of the population by affecting the innate capacity of the insect for increase, which is calculated from the rate of development, the fecundity and the length of the reproductive period (Barlow, 1962 and Legay and De Reggi, 1964). From results obtained in the laboratory under different constant temperatures a theoretical number of the aphid in the field can be calculated without the effects of the controlling factors encountered in the field. Temperature affects the aphid population directly by affecting the rate of development, fecundity and longevity of the

individuals or indirectly by affecting the suitability of the plant as a host.

The effect of temperature on M. persicae has been examined in different localities; Weed (1927) and Barlow (1962) in U.S.A.; De Jong (1929) in Sumatra; Jenjves (1945) in Germany; Rattan Lal (1950) in India: Broadbent and Hollings (1951) in U.K.; . MacGillivray (1958) in Canada and Legay (1964) in France.

The present work is a study of the effects of different constant temperatures on a population of M. persicae.

B. EXPERIMENTS WITH LEAF-DISCS ON CULTURE SOLUTION.

The aphid was reared on the host plants, brussels sprouts and potatoes, using leaf-discs floated on culture solution (Hughes and Woolcock's (1965) method). Another experiment was also done to test population development on potted plants of the two hosts. The latter experiment is discussed under another subheading.

(1) Materials and methods.

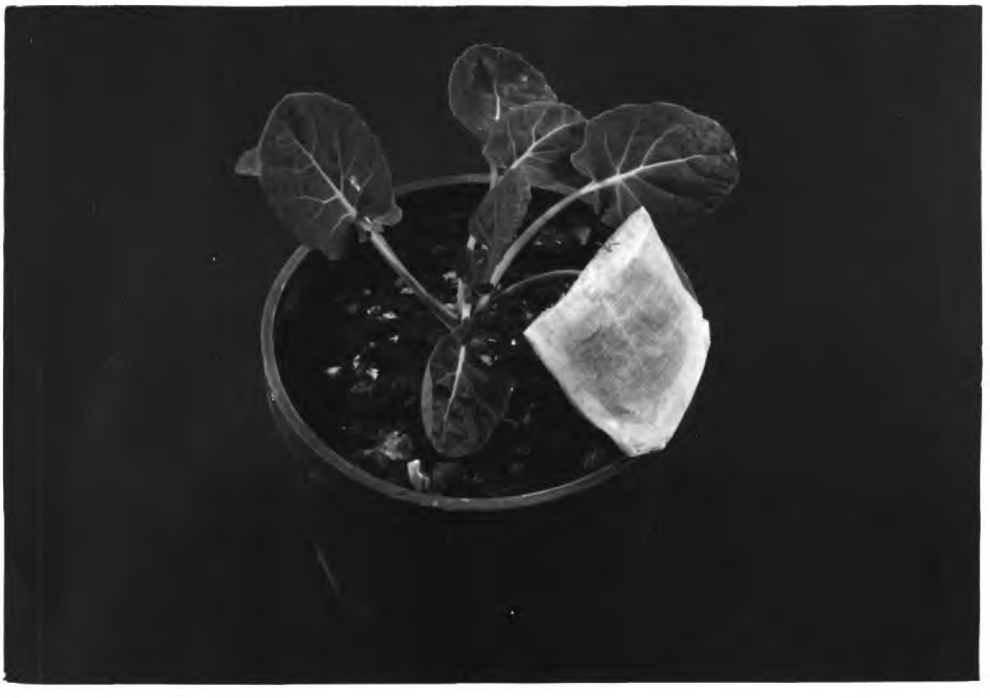
The experiment with the brussels sprouts leaf-discs was done at 10, 15, 20, 25 and 29°C , that with the potato leaf-discs at 15 and 20°C. There was artificial illumination for 16/24 hours and the relative humidity ranged from 45 to 75%. The individuals used in these experiments were taken from cultures maintained at the appropriate temperature on potted brussels sprout plants and potato

plants for about one month beforehand. In each room about 50 (2"x1") sample tubes were filled to within ¼" from the top with the culture solution. Mature leaves of brussels sprouts growing in the field and of potted potato plants growing in 15 and 20°C controlled environment rooms were used for the leaf-discs. Choice of mature leaves minimized the effect of leaf age on the insect (Kennedy, Ibbotson and Booth, 1950; Heathcote, 1962 and Muller, 1966). As M. persicae is a restless insect (Banks, 1965; Van Emden, 1966) especially at high temperatures the sample tubes were kept within a small distance of each by inserting in a honey-comb (plate 1) set in a plastic box filled with water. Wandering aphids were stopped by the water in the plastic box and they returned to the appropriate leaf-disc. This is a useful improvement to the Hughes and Woolcock (1965) method.

About three adult apterae were transferred to each leaf-disc and in each room the plastic boxes holding the tubes were covered with glass sheets. After 3 hours the adult apterae and excess progeny were removed leaving a single newly born nymph on each disc. Observations were made at 3 hours intervals except between 1a.m. and 9a.m. Exuviae were recorded and removed. After maturation daily observations were made and newly born nymphs were counted and removed. The leaf-discs were replaced by fresh ones at least once a week. Culture solution in the tubes and water in the plastic boxes were topped up as required.

Plate 1. Leaf-disc on culture solution technique for the biological study of M. persicae.

Plate 2. Leaf cage for the assessment of mortality of the immature stages of M. persicae on brussels sprouts.



An attempt was made to find the duration of the winged fourth instar nymph at the different temperatures. Too few winged third instars were however available except at 10°C and 15°C. The procedure used was the same as for the apterae. Single winged late third instar nymphs were gently transferred to leaf-discs and at 15°C observations were made at 3 hours intervals between 9am. and 9a.m. At 10°C observations were made twice daily until the individuals became adults.

Mortalities in the nymphal stages at the different temperatures and on the two host plants were determined. Potted plants of brussels sprouts and potato were kept at the appropriate constant temperatures for about a week before the experiment commenced. Small organdie cages were used. Adults maintained on the two host plants were transferred to the lower surfaces of leaves, enclosed in clip-on cages and left for 24 hours, after which they were removed. Leaves and leaflets of brussels sprout and potato respectively each supporting about 10 nymphs were very carefully inserted inside the organdie cages without disturbing the aphids, the open ends glued together and any apertures between the petioles and cages were plugged with cottonwool (plate 2). About 100 nymphs were caged in each room. After the elapse of the developmental period under each temperature, the cages were cut open, the number attaining maturity counted and the % of mortality under the different temperatures estimated. The death was assumed to have occurred mid way between birth and maturity.

The intrinsic rate of increase denoted by (r) and known as Malthus constant was calculated. This parameter is also the natural log. of the finite rate of increase which is defined as the number of times a population will increase in a unit time. The method used is the one described by Birch (1948) and by Leslie and Park (1949) working on stored products pests. A preliminary intrinsic rate (r) was calculated from the equation

$$\frac{Nt + 1}{Nt} = e^{r}$$

where Nt is the number of insects at time t and Nt + 1 the number of insects one unit of time later. Then an accurate value of 'r' which best satisfies the equation below was calculated by trial and error substitution:

$$\sum e^{-rx} Lx\, Mx = 1$$

where x = the midpoint of each age group

Lx = the survival rate

Mx = the age specific fecundity rate.

Also the method provided a useful tool by which the number of times a population will multiply in one generation denoted by R_0 could be calculated. This is determined by summing up Lx Mx for each age group for values of Mx $>$ 0. Summing up of Mx alone for all the age groups is referred to as the gross reproduction rate.

(2) Results.

(a) Rate of development.

Tables 11 and 12 present summaries of the results obtained under the five and the two constant temperatures on brussels sprouts and potatoes respectively. It is descernible that any rise in temperature between 10-29°C was followed by a fall in the duration of the development (tables 11 and 12). However, the difference in developmental periods resulting from 5°C rise at the lower temperatures of the experiment was high and this difference tended steadily to diminish until the difference was only about 12 hours with the temperature rise from 25 to 29°C. This implied that any further rise in temperature might have a retarding effect on the rate of development. Correlation coefficients calculated for the sets of figures including and excluding the 29°C were -0.932 and -0.965 respectively. Both were significant at $p = < 0.05$.

At corresponding temperatures, the proportional lengths of the different instars bred on the two host plants were almost equal. Table 12 shows ratios of the various instar durations to that of the first instar at the five and two constant temperatures. Among the four instars, the fourth was of longer duration, the third and the second were the shortest and were almost equal to each other, while the first was very slightly longer that the second and the third. The total times for development in the two host plants were almost equal at the 20°C constant temperature, but 1.49 days

Table 11. Effect of temperature on the various functions of *M. persicae* reared on brussels sprouts leaf-discs.

Temp. (°C)	Duration in days of the										Fecundity	Nymphs/female/day	Intrinsic rate of increase (r)	Finite rate of increase (λ)	Rate of multiplication/ generation (Ro)
	First instar	Second instar	Third instar	Fourth instar	Total development	Pre-larviposition	Maturation	Reproduction	Pre-death	Longevity					
10	5.01	4.54	4.53	5.79	19.87	2.09	21.96	14.42	4.21	20.72	19.5	1.35	0.57	1.8	11.4
15	2.91	2.80	2.84	3.27	11.82	1.07	12.89	12.77	2.40	16.24	36.7	2.87	1.1	3.0	28.42
20	2.11	1.68	1.73	2.09	7.61	0.72	8.33	12.39	2.10	15.21	46.6	3.49	1.5	4.4	37.45
25	1.49	1.31	1.38	1.62	5.80	0.66	6.46	12.25	1.83	14.74	53.6	4.37	1.8	6.0	34.64
29	1.32	1.23	1.26	1.50	5.31	0.79	6.10	6.74	3.40	10.93	17.6	2.60	1.3	3.7	7.84

Table 12. Effect of temperature on the various functions of M. persicae reared on potato leaf-discs.

Temperature °C	Duration in days of the										Fecundity	Nymphs/female/day	Intrinsic rate of increase (r)	Finite rate of increase (λ)	Rate of multiplication/ generation (Ro)
	First instar	Second instar	Third instar	Fourth instar	Total development	Pre-larviposition	Maturation	Reproduction	Pre-death	Longevity					
15	2.65	2.26	2.44	2.99	10.34	1.03	11.38	22.00	7.67	29.67	72	3.27	1.25	3.5	54.85
20	1.98	1.75	1.80	2.30	7.84	0.86	8.70	14.83	3.74	18.56	57	3.84	1.50	4.4	32.70

shorter on potatoes at 15°C (difference significant at $p = < 0.01$).

Fig. 4 shows the relation between temperature and the duration and rate of development at the five temperatures on brussels sprouts. The developmental period showed a curvilinear relation while the rate of development and temperature followed a sigmoid curve. When the rates of development were plotted against temperature on log. paper (fig. 5) the points at the lower 4 temperatures fell in a virtually straight line. The values at these 4 temperatures were used to calculate the regression of rate of development on temperature.

Table 13. Ratios of instar durations to that of the first instar reared on brussels sprout and potato leaf-discs.

Temp. °C	Brussels sprouts				Potatoes			
	INSTAR				INSTAR			
	First	Second	Third	Fourth	First	Second	Third	Fourth
10	1.00	0.91	0.91	1.15				
15	1.00	0.96	0.97	1.12	1.00	0.85	0.92	1.13
20	1.00	0.80	0.82	0.99	1.00	0.88	0.91	1.16
25	1.00	0.88	0.93	1.09				
29	1.00	0.93	0.95	1.14				

The relation between the rate of the development of the four nymphal instars and temperature was then calculated. Fig. 6 shows that this followed a straight line for the 4 stages of development. According to Bodenheimer and Swirski (1957) working on several aphid

Fig. 4. Effect of constant temperatures on period and rate of development of M. persicae (Sulzer).

Fig.4.

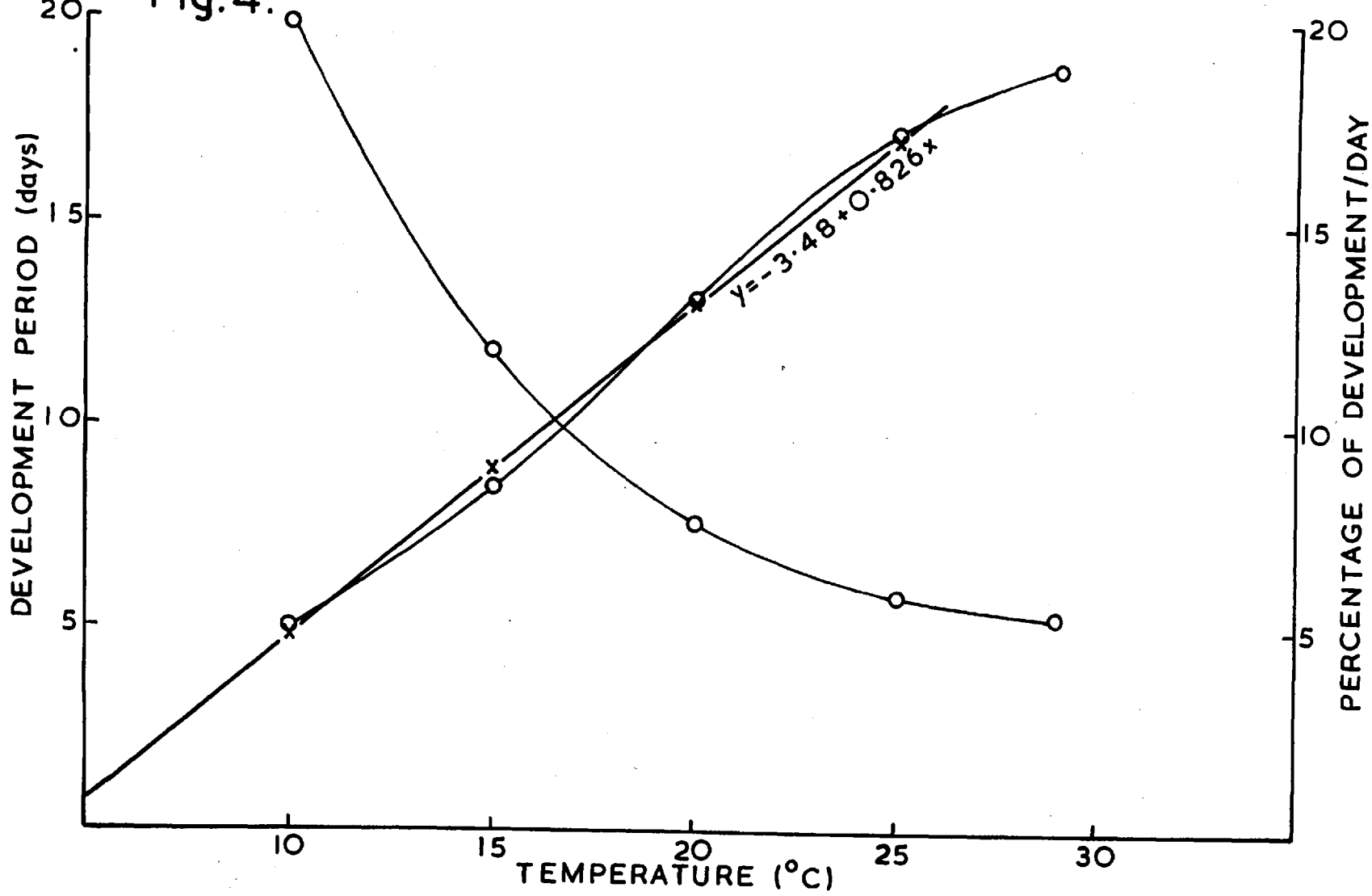

DEVELOPMENT PERIOD (days)
PERCENTAGE OF DEVELOPMENT/DAY
TEMPERATURE (°C)
Y=-3·48+0·826x
20
15
10
5
10
15
20
25
30

Fig. 5. Relation between constant temperature and rate of development on logarithmic scale.

Fig.5.

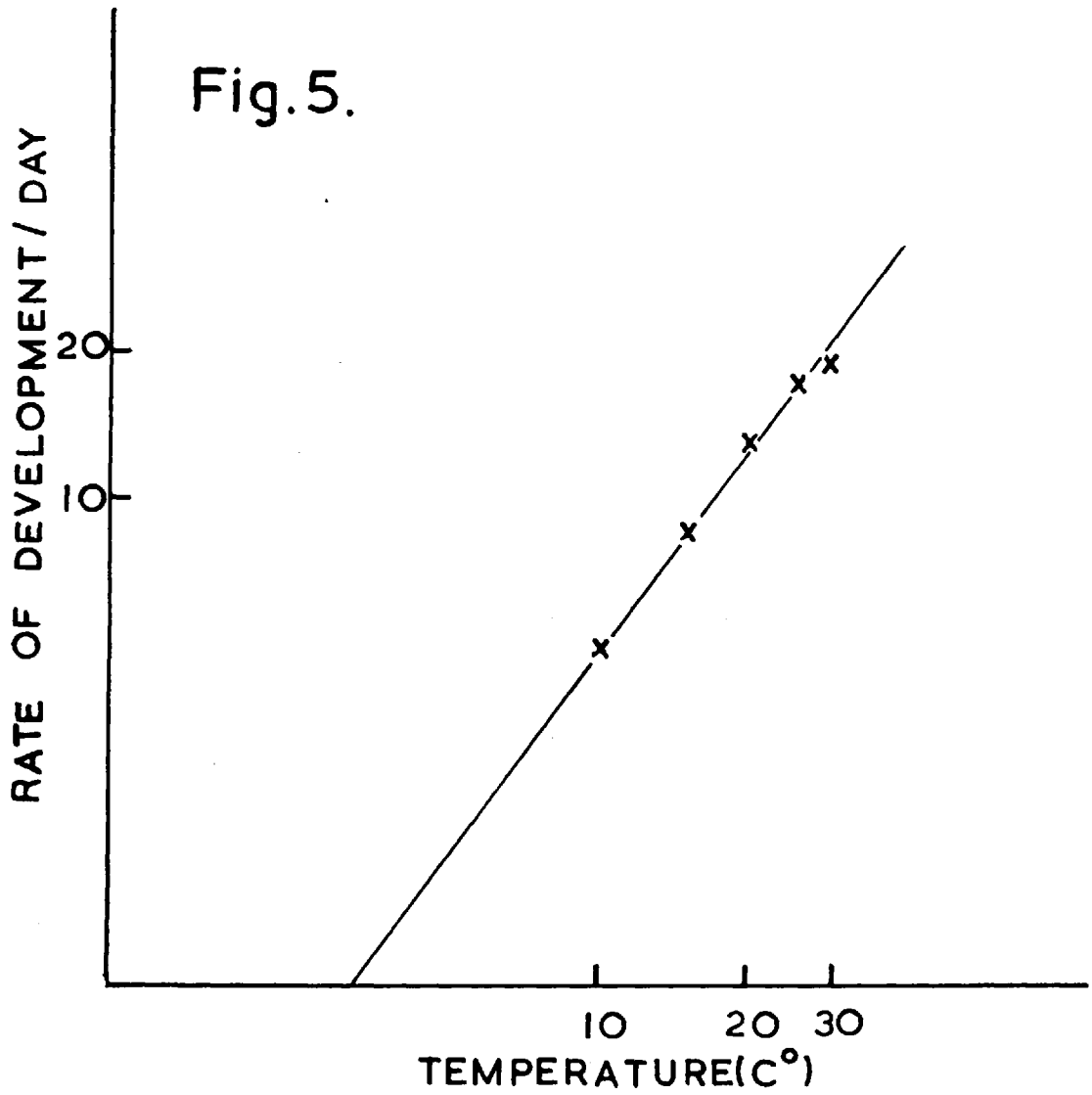
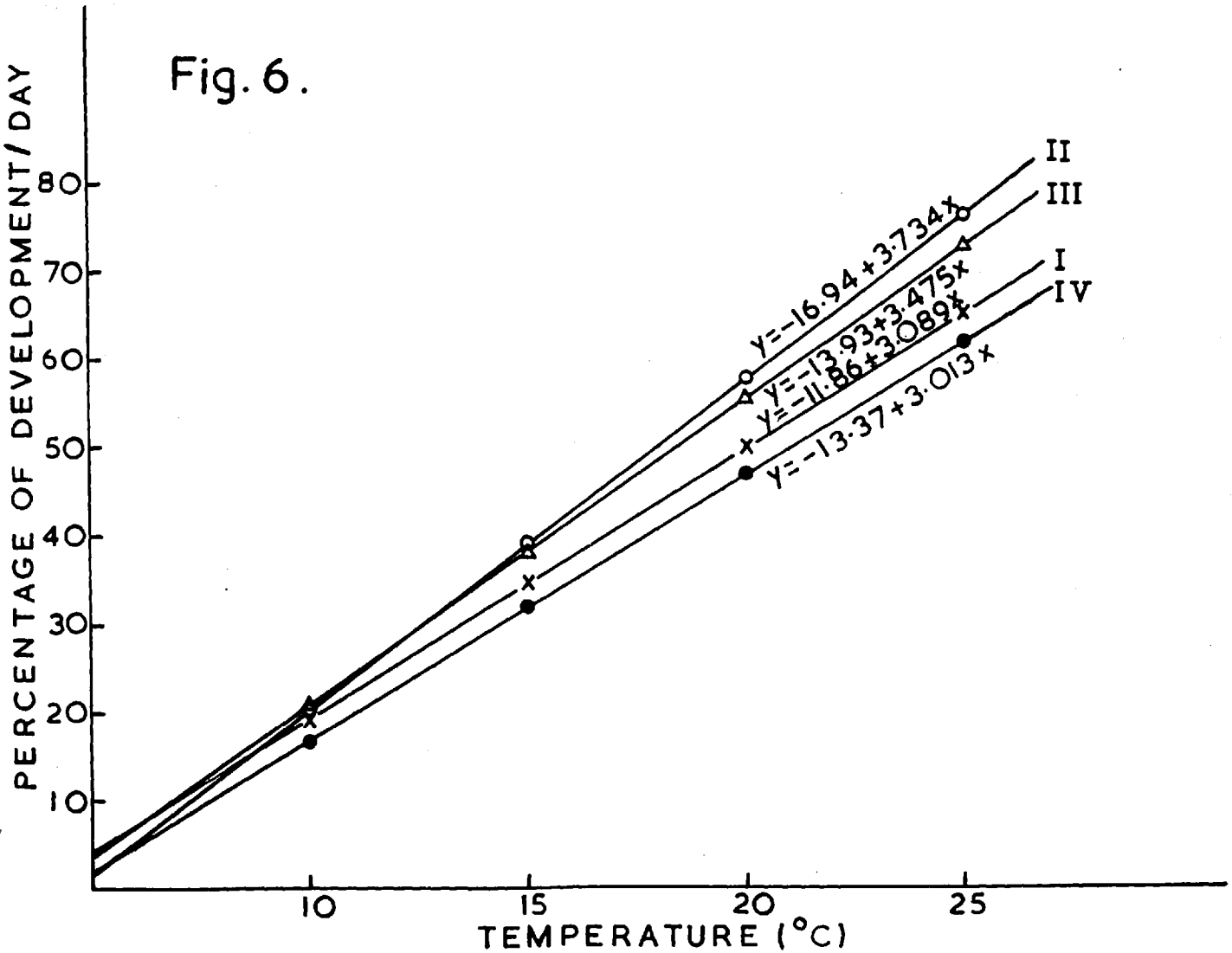


Fig. 6. Rate of development of the four nymphal instars at different constant temperatures.

Fig. 6.


PERCENTAGE OF DEVELOPMENT / DAY
80
70
60
50
40
30
20
10
10
15
20
25
TEMPERATURE (°C)
II
III
I
IV
Y=-16.94+3.734x
Y=-13.93+3.475x
Y=-11.86+3.089x
Y=-13.37+3.013x

species and Hughes (1963) on Brevicoryne brassicae (L.) the rate of development is proportional to the temperature above the threshold value (K). This threshold was estimated in this work to be 3.84, 4.54, 4.01, 4.44 and 4.21 for the first, second, third, fourth instars and adult apterae respectively. The product of temperature above (K) and the developmental period is considered to be constant and is known as thermal constant. Such results can be used to estimate the developmental period of all the stages within temperatures varying from 10°C to 25°C. The figures were 774, 641, 690, 795 and 2899 hour-degrees C° for the 1st, 2nd, 3rd, 4th instars and adult apterae respectively.

The durations of the alate fourth instar at 10°C and 15°C were 8.50 and 5.42 days respectively. They were longer than the durations of the corresponding apterae. The pre-larviposition period followed the same pattern as the developmental period up to 25°C. At 29°C it was 3 hours longer than at 25°C.

(b) Fecundity.

The average number of births per female and the rate per female per day of the individuals bred on brussels sprouts leaf-discs rose steadily with rise in temperature and reached a maximum at 25°C. A sharp drop resulted at 29°C (table 11). Fig. 7 (A-E) shows age specific fecundity rates, each point indicating the number of young born per week per female alive at the mid-point of each week. At 10°C the young were deposited over a long period (about 3 weeks) with two small peaks, the bigger one being after the 6th week.

Fig. 7. Survival and fecundity rates of M. persicae on brussels sprouts leaf-discs at the five constant temperatures.

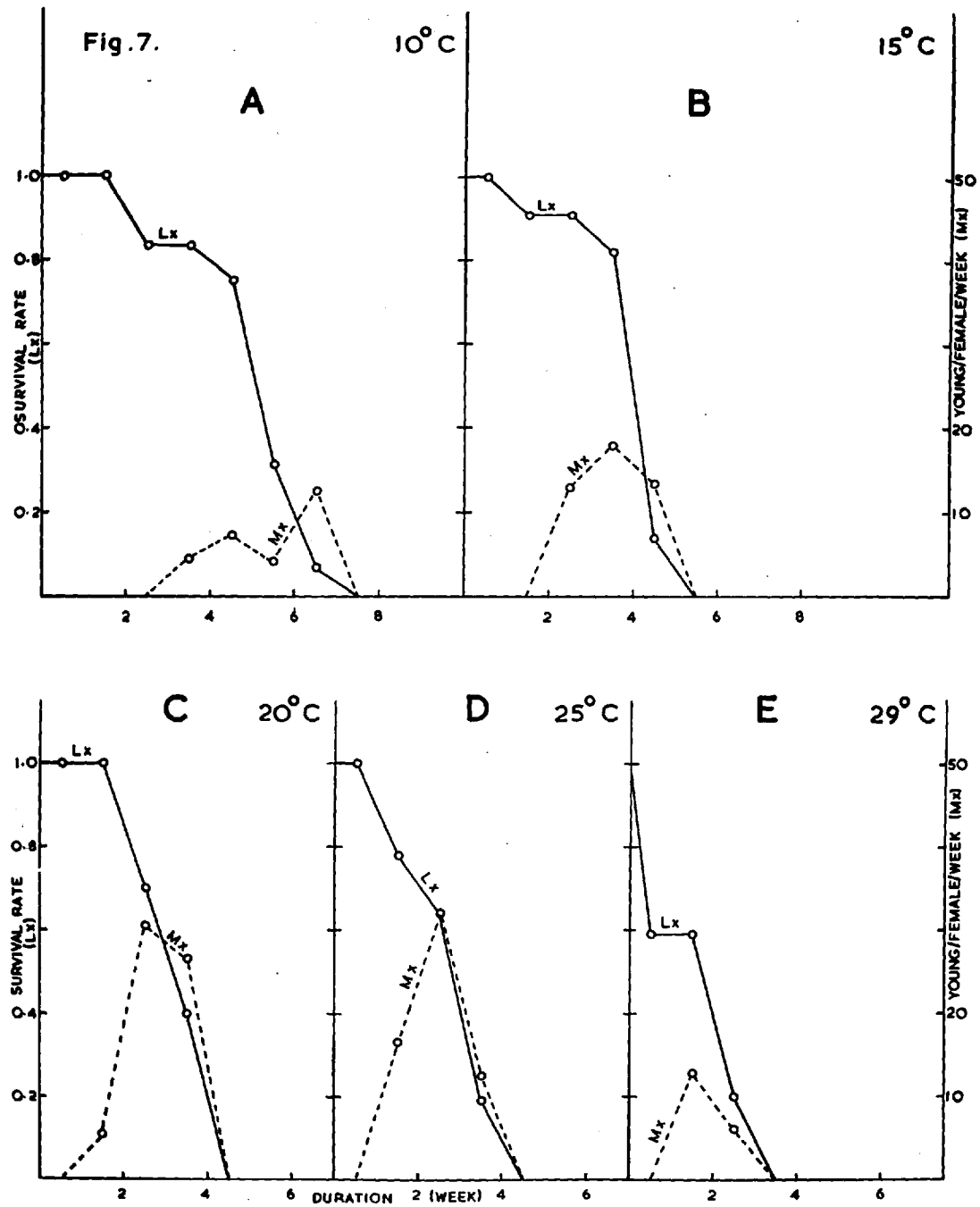


Fig.7.
10°C
15°C
A
B
C
D
E
20°C
25°C
29°C
Lx
Mx
SURVIVAL RATE (Lx)
YOUNG/FEMALE/WEEK (Mx)
DURATION (WEEK)

At 15°C reproduction started earlier and lasted for a shorter period (2 weeks) with a peak after the 3rd week. At 20 and 25°C the peaks of reproduction were reached at the same time (2.5 weeks) being slightly higher and sharper at the latter temperature. At 29°C the peak of reproduction, which was a small one, was reached after the first week and was then followed by a sharp drop. The duration of the larviposition period was negatively correlated with temperature, the drop being sharp at 29°C (table 11).

More young were deposited on the potato leaf-discs at 15°C than at 20°C, thus showing a different pattern to the one on brussels sprouts; also more were produced on potato than at the corresponding temperature on brussels sprouts, the increase being about 100% and 20% at 15°C and 20°C respectively. Fig. 8 (A and B) shows the mean weekly rates of reproduction. The peak of reproduction was in the fourth week at 15°C and slightly before the 4th at 20°C. The reproduction period was also longer than on brussels sprouts especially at 15°C where it was about 80% longer.

(c) Longevity.

Mortalities during the nymphal development on brussels sprouts were 16.7, 8, 0, 28 and 41% at 10, 15, 20, 25, and 29°C respectively. Fig. 7 (A-E) shows the longevities of the individuals started with as survival rates at the different constant temperatures. Each point represents the number of females alive at the mid-point of each week. This is plotted as the proportion of the 100 nymphs with which the

Fig. 8. Survival and fecundity rates of M. persicae on potato leaf-discs at 15 and 20°C.

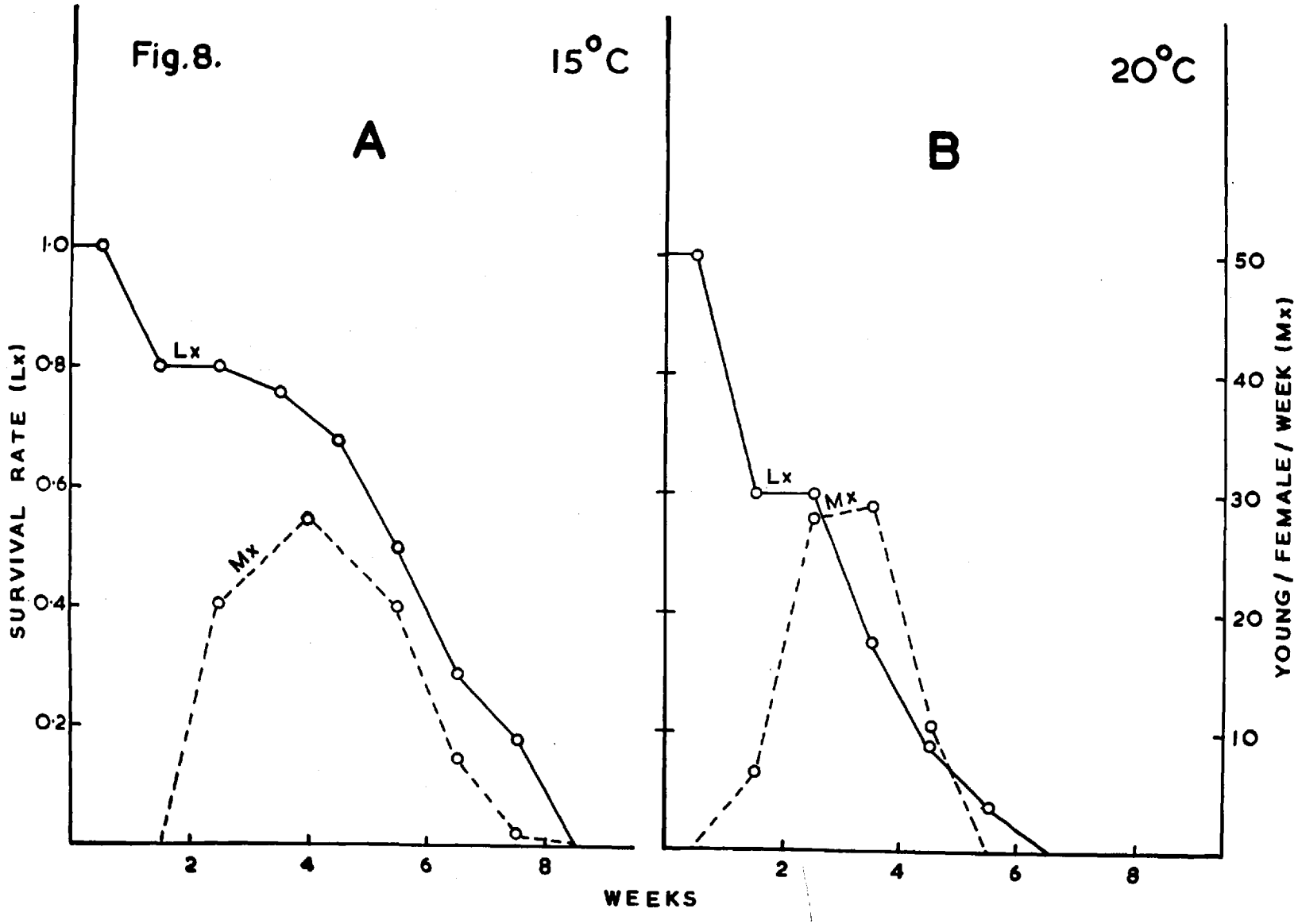


Fig.8.
15°C
20°C
A
B
SURVIVAL RATE (Lx)
YOUNG / FEMALE / WEEK (Mx)
Lx
Mx
1·0
0·8
0·6
0·4
0·2
50
40
30
20
10
2
4
6
8
WEEKS

experiment was started. The results also showed a negative correlation with the temperature (table 11).

Mortalities in the nymphal stages on potatoes was considerably higher than on brussels sprouts, the percentages being 20 and 40% at 15 and 20°C respectively. The longevities followed the same trends as on brussels sprouts but were greater on potato especially at 15°C. Fig. 8 (A and B) shows the survival rates of the population at different ages. At 15°C 50% mortality of the total number occurred after $5\frac{1}{2}$ and 4 weeks on potatoes and brussels sprouts respectively, although at 20°C it occurred in about 3 weeks on both host plants. On both hosts the pre-death period decreased steadily with rise in temperature to 25°C but at 29°C an opposite reaction was indicated (tables 11 and 12).

(d) The intrinsic rate of increase.

The intrinsic rate and the finite rate of increase exhibited a positive correlation with temperature up to 25°C on both host plants but in contrast ~~relative~~ to the lower temperatures it was negatively correlated with temperature at 29°C. At 15°C the calculated rates of increase on potato were slightly greater than on brussels sprouts. On brussels sprouts the rate of multiplication per generation (R_o) attained its maximum at 20°C and decreased above and below this temperature; but on potatoes it was greater at 15°C than at 20°C and at this temperature (15°C) it was about double the figure on brussels sprouts.

C. POPULATIONS ON POTTED PLANTS.

(1) Introduction.

The population study of Myzus persicae on potted plants of brussels sprouts, Brassica oleracea gemmifera and potatoes, Solanum tuberosum, variety Majestic was done at 15 and 20°C constant temperatures. The two species are important secondary hosts and can support large populations of the aphid in the field when conditions are favourable. Shaw (1955a)and Broadbent and Heathcote (1955) reported that in England aphids from overwintering secondary hosts play a bigger role in infesting crops in spring than do aphids from peach, the primary host. Heathcote (1962) examined the value of a wide range of secondary hosts of M. persicae and concluded that the aphid did well on Brassica spp.but less well on sugarbeet, spinach and lettuce.

The following experiments aimed at comparing the suitability of brussels sprouts and potatoes by breeding the aphid on leaf-discs floated on culture solution as used by Hughes and Woolcock (1965), and also on potted plants of the two species watered with tap water. Information on the effect of different nutrients on the aphids is reported by various authors. Vijverberg (1965) working on M. persicae on potato recorded an increase in infestation when the aphids were reared on plants receiving high N/K ratios. Dadd and Mittler's (1965) results showed that K, Mg and P were essential for adult survival and larviposition. Van Emden (1966) comparing the

reproduction of Brevicoryne brassicae (L.) and M. persicae on brussels sprouts supplied with different rates of nitrogen and potassium reported that an increase in N or decrease in K resulted in an increase in soluble nitrogen level and that the fecundity of M. persicae showed a positive correlation with this, while B. brassicae showed a markedly smaller response. These results contradicted those of Michel and Chouteau (1963) who reported that the fecundity of M. persicae bred on leaf-discs cut from tobacco plants grown in nutrient solution was increased by K and decreased by N. This difference and other conflicting results could possibly be due to the different plant or aphid species used, the different formulations of the nutrients or the differences between experiments in the field and laboratory. A more convincing explanation could be attained if such studies included investigations of changes in the plants caused by the nutrient treatments (Van Emden, 1966).

The study of population growth in the laboratory on potted plants eliminated the impact of factors encountered in the field such as drought, natural enemies and heavy rains. Thus the 'free' progress of the population is obtained by counting at intervals. From the data on leaf-disc experiments, a theoretical population growth under uncrowded conditions can be calculated. The comparison of the observed on the potted plants and the calculated population could indicate the stage in population growth at which the aphids mutually benefit from each other and also the stage when the

population is large enough for the individuals to begin to compete with each other for food and or space. This stage is marked by slowed rate of reproduction and increased developmental mortality (Way and Banks, 1966; Way, 1968).

An aphid species maintained on a particular host plant might be deleteriously affected when transferred to a different species of host plant. Heathcote (1962) while culturing all his aphids on turnips, Brassica campestris rapa reported, nevertheless, that it was likely to be more unsettling for an aphid to be moved from one host species to another species than to be moved from one variety of a species to another. In this experiment, the population growth on potatoes and brussels sprouts of aphids maintained previously on brussels sprouts and potatoes was investigated i.e. aphids were transferred to the other host plants as well as to the same one.

(2) Materials and methods.

The constant temperature rooms in this experiment were the same as already described. In the two rooms apterous females from a population maintained on brussels sprouts were transferred to 2 fresh brussels plants, left overnight to reproduce and then removed. About 60 of their nymphs were allowed to develop to maturity. In each room 10 brussels and 10 potato plants initially about 6" tall were kept for about one week and then a single newly matured adult from brussels sprouts was transferred to each. A cellulose acetate ring, about 1" high with fluon applied to its inner wall, was placed

round the plant to stop dislodged aphids from crawling away. The plants were then transferred to Watkins and Doncaster cages. Daily observations were made for the first few days to ensure that the aphids had settled. Later, counts of the aphid numbers were made twice a week for 3 weeks.

Another set of experiments was done in the same two rooms using the same procedure as above except that the culture was maintained on potato plants for two months before the aphids were used. The plants were watered with tap water twice a week.

(3) Results.

Table 14 presents a summary of the results. It can be seen that brussels sprouts is a more suitable host than the potatoes; the mean numbers (A compared with F at 20°C; C compared with H at 15°C) on the brussels being significantly more at $p = < 0.05$ level at both temperatures. With aphids initially cultured on brussels sprouts (A compared with B at 20°C; C compared with D at 15°C) the differences when transferred to brussels and potatoes were significant at $p = < 0.001$ level at both temperatures. The difference being significant at $p = < 0.001$ level under I and at $p = < 0.05$ level when aphids were transferred from the same plant implied that transferring aphids maintained on brussels sprouts to potato slowed the rate of multiplication. The reverse of this is not true since (E) population was higher on brussels plants infected with individuals maintained on potatoes than those infected with individuals maintained on brussels (A).

Table 14. The mean numbers of M. persicae after three weeks in the various treatments.

I Original culture on brussels				II Original culture on potatoes			
20°C		15°C		20°C		15°C	
Brussels (A)	Potato (B)	Brussels (C)	Potato (D)	Brussels (E)	Potato (F)	Brussels (G)	Potato (H)
544±68	55±20	205±34	29±9	864±140	377±18	143±16	105±15

It was noticed that temperature 15°C was more favourable for the potato plant than 20°C. At the former they were healthier and were giving continuous fresh growth, whereas at 20°C growth was slow.

Fig. 9 shows the calculated and observed numbers of the aphids on the two host plants at the two constant temperatures. It can be seen that the calculated number is bigger than the observed in all treatments. The difference being greatest on both host plants at 20°C and on potatoes at 15°C. The calculated and the observed lines remained similar until the beginning of the second generation when they began to depart. At 20°C the calculated numbers were almost equal on both host plants. At 15°C the second generation started about $1\frac{1}{2}$ days earlier and the difference between the calculated and observed numbers was very large by the end of the experiment (Fig. 9D).

At 20°C the rate of progress of the population on one of the brussels plants was remarkably high. The final number was more than double the mean and about 5 times that on the lowest plant-population.

Fig. 9. The potential and observed growth of aphid populations on brussels sprouts and potatoes at 15 and 20°C.

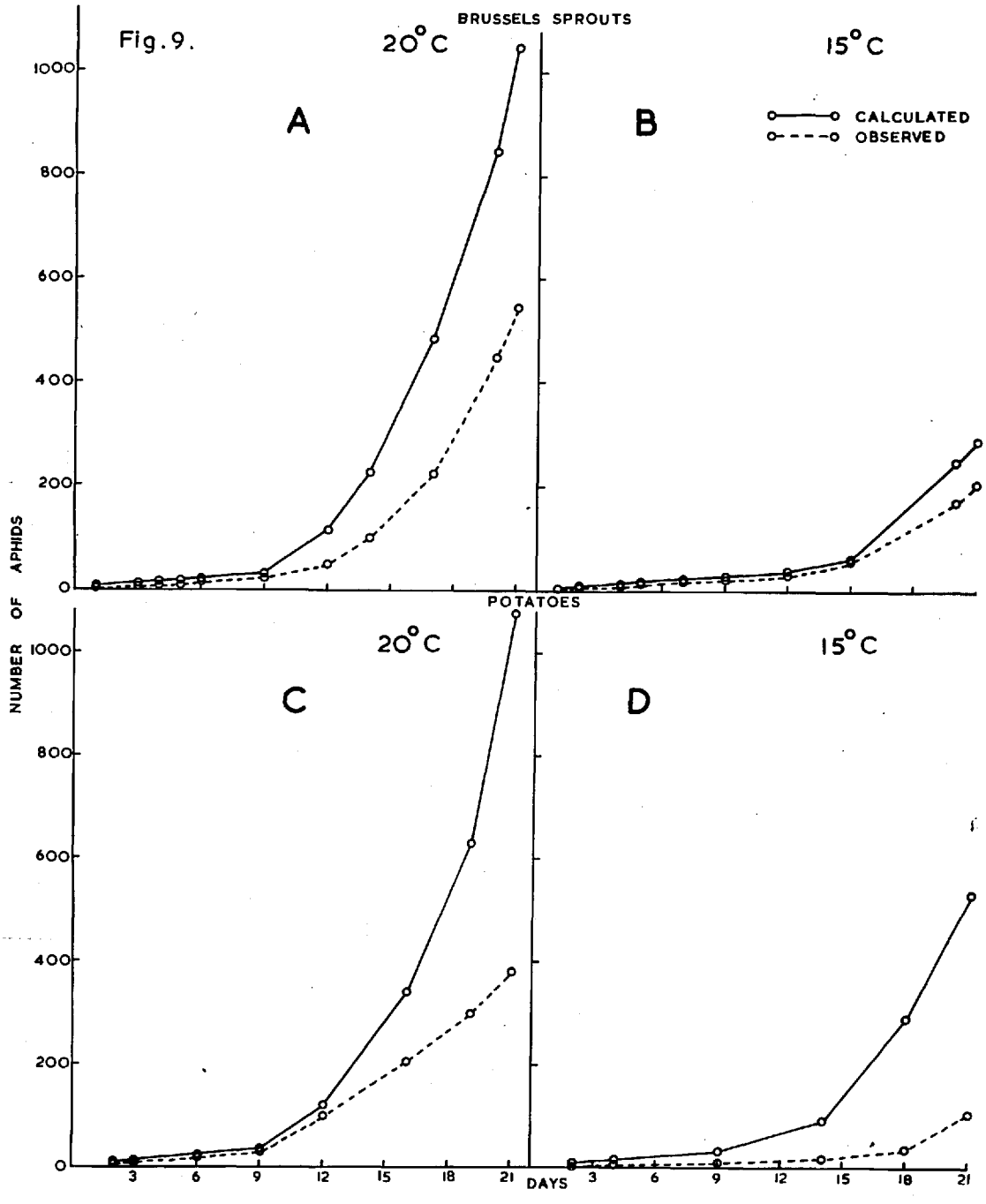


Fig. 9.
BRUSSELS SPROUTS
20°C
15°C
A
B
CALCULATED
OBSERVED
NUMBER OF APHIDS
1000
800
600
400
200
0
POTATOES
20°C
15°C
C
D
3
6
9
12
15
18
21
DAYS

The leaves of the plant were covered with rounded black spots, possibly a virus infection. The population development on this plant agrees with Baker's (1960) and Macias and Mink's (1969) reports that M. persicae preferred leaves of sugarbeet infected with virus to healthy ones and that they bred more rapidly and lived longer on them.

D. DISCUSSION.

(1) Leaf-disc experiments.

Results obtained on brussels sprouts at five constant temperatures, relative humidity ranging from 45 to 75% and 16/24 hours photoperiod, indicate that temperature, by regulating the rate of development, fecundity and longevity of M. persicae, controls its innate capacity for increase.

The rate of development from birth to adult increases with rise in temperature between 10 and 29°C, the duration ranging from 19.87 to 5.31 days. Table 15 shows a summary of the development period reported by previous authors and that obtained at the present work. Weed's (1927) results, for the first four temperatures, agreed basically with the current findings, but at 28°C the duration was longer than at 24°C, which contradicts the present result. Weed made no mention of culture conditions of the insects before the commencement of the experiment, but the fact that the duration of the first instar was shorter at 28°C than at 24°C, while those of

other 3 instars were longer, suggests that the individuals he used were not acclimatized to the temperature before the start of the experiment. De Jong (1929) reported that M. persicae completed development in 7 days, a figure which is longer than in the present work. Lal (1950) experimented on the effect of three temperatures. His figures, although less than the ones at present, nevertheless follow almost the same trend. Barlow's (1962) figures at 10, 15, 20 and 25°C were remarkably short compared with the present data especially at 15°C (table 15). He also stated that the aphid failed to develop at 30°C.

Table 15. Summary of results by various authors on development period. (Temperature in °C in parenthesis.)

Author	Host plant	Temperature and development period (days)				
Weed(1927)	Spinacia sp.	20.8(10)	11.4(16)	8.3(21)	6.5(24)	7.2(28)
De Jong(1929)	Ipomoea sp.					7.0(30)
Lal(1950)	Brassica sp.			7.0(18)	6.5(26)	4.3(30)
Barlow(1962)	Nicotiana sp.	16.8(10)	6.3(15)	4.9(20)	4.2(25)	- (30)
Present author	Brassica sp.	19.9(10)	11.8(15)	7.6(20)	5.8(25)	5.3(29)

In the present experiments the larviposition period followed the same trend as the developmental rate, the shortest being at 29°C (table 10). The fecundity was least at 29°C and steadily increased from 10 to 25°C (table 10). The number of progeny per female per day were 1.3, 2.9, 3.5, 4.4 and 2.6 nymphs at 10, 15, 20, 25 and 29°C respectively. This agrees with Weed's results which were 1.8, 2.6,

3.2, 3.7 and 3.0 nymphs/female/day respectively. Different authors' results however vary. Lal (1950) recorded 30.5 and 28.9 nymphs as the average per female at 30°C and 26°C respectively, the former being much more and the latter much less than the present results. Heathcote (1962) quoted 17 nymphs/female at 20°C which is less than half the value obtained by the writer.

The calculated intrinsic rates of increase at constant temperatures of 10, 15, 20, 25 and 29°C are 0.57, 1.1, 1.5, 1.8 and 1.3 respectively. These values depend on nymphal development period, fecundity, larviposition period and mortality in the immature stages. The maximum rate of reproduction and the age at which this is attained is a more important factor in conditioning (r) than total nymphs deposited through the whole life span; therefore, only the progeny in the first few weeks have a sizeable effect on (r) and (Ro). From table 11 and fig. 7C & D it can be seen that although (Ro) at 20°C is more than at 25°C, yet (r) at the latter temperature is more. This is partly due to more progeny being born in the first two weeks at 25°C.

The values of (r) presented by Barlow (1962) were 0.84, 2.38, 3.13, 3.15 and - ∞ at 10, 15, 20, 25 and 30°C respectively. These figures, although they agree in general trends with the present result from 10 to 25, are remarkably larger. However, the present results almost agree with the findings of Leggy and De Reggi (1965) whose values for (r) were 2.1 - 2.3 on old cabbage leaves and 1.3 - 1.9

on young cabbage plants at 20°C. This indicates that apart from temperature, the stage of growth of the host plant greatly affects the value of (r). In the light of results obtained here and those cited by Barlow it is concluded that 25°C is the most suitable of the constant temperatures tested for rapid population growth of M. persicae.

Conflicting results presented in the foregoing discussion could be because the different authors used different plant species or because M. persicae is a sensitive insect affected by slight changes in the environment or it comprises biological races which react differently to the same environment.

Results with brussels sprouts and potatoes exhibited interesting differences (tables 11 and 12). At 20°C development was completed on average about 5 hours quicker on brussels, while at 15°C it was about 36 hours slower than on potato. The larviposition period and longevity on brussels was less than on potato at both temperatures, the differences being highly significant at 15°C ($p < 0.001$). Fecundity also followed the same trends and on potato it was about 100% and 20% more at 15°C and 20°C respectively (tables 11 and 12). To summarise, it appears that the potato leaf-disc was more suitable than brussels sprout leaf-disc for these processes especially at 15°C.

(2) Populations on potted plants.

After 21 days the population was greater on potted brussels sprouts than on potatoes at the two temperatures (table 14 and fig. 9),

The very slow rate of multiplication when the individuals were transferred from brussels to potatoes (table 14B and D) and the unaltered rate when opposite transfer was made may be of practical importance. The plant on which the aphids overwinter as viviparous females may for example affect the size of the aphid population on other commercial crops. During the experiments it was observed that individuals transferred from brussels sprouts to potato were restless and did not settle except after much wandering during which some were lost and had to be replaced. After the opposite transfer the individuals initially found it difficult to grip the leaf of the brussels, but soon settled and started reproducing.

(3) Comparison of populations on leaf-discs and potted plants.

Population counts on potted plants indicate that brussels sprout is a more suitable host plant than potato at 15 and 20°C (table 14). Data presented in tables 11 and 12 using leaf-discs on culture solution show the opposite i.e. potato is the more suitable host. The apparent difference between the two treatments is that in the first condition whole potted plants with young and mature leaves were supporting the population, whilst in the second, leaf-discs from a mature leaf floating in nutrient solution supported the aphid. The nutrient materials included calcium, potassium, magnesium, phosphorus, iron, sulphur and nitrogen (Hughes and Woolcock, 1965). Vijverberg

(1965) and van Emden (1966a) working on M. persicae on potato and brussels respectively reported that treating the plants with N and K increased the fecundity of the aphids. The present results demonstrate that at 20°C the aphids on potato leaf-discs were more fecund than on brussels sprouts, although the developmental period was slightly longer on the latter. This suggests that potato has benefitted more than brussels from the nutrients. The results at 15°C further confirm this because the aphid has a remarkably shorter developmental period and greater fecundity on potatoes. This is in agreement with the observation that at 15°C, but not at 20°C, potato plants produced fresh growth continuously and that the leaf-discs on the culture solution increased in size and developed adventitious roots.

The potential rates of increase calculated from the data on leaf-discs of the two host plants and the observed rates on potted plants of the two species at the two constant temperatures indicate that the two populations differ in size (fig. 9). The difference was greater on potatoes particularly at 15°C. This discrepancy could be attributed to a possible difference in the relative suitability of the whole plant and the leaf-disc on culture solution to the aphid. This is particularly true at 15°C where the population was probably not large enough on potted plants to cause intra-specific competition especially with M. persicae which does not occur in compact colonies. However, at 20°C where the populations rose in 21 days to 544 and 377 on small brussels and potato plants respectively, the number possibly

increased enough to initiate competition between the individuals and lead to the deterioration of their quality. Therefore, the difference at this temperature might, at least in part, be due to competition. Further work is needed to clarify these points.

SECTION III. THE EFFECT OF CRITICALLY HIGH AND LOW TEMPERATURES ON MYZUS PERSICAE SULZER.

A. INTRODUCTION.

Temperature is important in determining size, fecundity, longevity and rate of development in insects. The latter 3 physiological characters are especially important parameters influencing the intrinsic rate of increase in insects. Size which is reduced under unfavourably high and low temperatures has also an indirect effect (Murdie, 1965) since it has been shown to be positively correlated with fecundity. A long exposure to high or low temperatures can alter the insects response to other temperatures. Therefore, the knowledge of the thermal history of an insect is important and may perhaps explain contradictory results that have been obtained with M. persicae, for example (Lal, 1951 and Barlow, 1962).

Most of the work done on this line has involved examining the effect of temperature for one generation. No detailed studies seem to have been made on the effect of critically high and low temperatures on successive generations of insects or on their recovery when returned to favourable temperature conditions. Murdie (1965) has, however, produced some relevant data using the aphid, Acyrthosiphon pisum (Harris). The experiments described in this section were designed to study the effect of critically high and low temperatures on several successive generations of M. persicae. Such information

is particularly important for understanding the dynamics of . M. persicae in the parts of its distribution range with cold winters e.g. North and South temperate regions or hot summers e.g. places with Continental, Mediterranean or Tropical climate.

B. REVIEW OF LITERATURE.

(1) Acclimatization.

Climatic regions influence, through various factors, the number and species of insects within them, their abundance and distribution. Seasonal and local variations of some of these factors within these regions, temperature being of major importance, cause intraspecific variations in insedt size. However, previous observations indicate that a species can move from its habitat and spread to another which was previously too cold or too hot (Uvarov, 1931). An example was cited by Hinds (1907) in connexion with the gradual extension of the range of the cotton-boll weevil from Mexico to the United States.

Shelford (1929) distinguished two concepts, acclimatization and acclimation. By the latter term he meant the adjustment in constitution or response of an individual transferred to a set of conditions, while acclimatization meant the changes resulting from a long exposure involving several generations. But Uvarov (1931) stated that there was no difference between the two terms, since acclimatization to new conditions cannot be expected unless the individuals subjected to the new conditions can survive and reproduce under them. Smith (1957) working on Drosophila subobscura reported that temperature during pre-adult life had a more"long lasting" effect on the capacity of adults to withstand exposure to high temperatures than the relatively short exposure of the adult life itself. He classified these as developmental and physiological acclimatizations respectively.

First records on this phenomenon were made from the natural habitats of insects. Bremer (1928) reported that a mild and wet autumn followed by a sudden frost was more injurious to several insect species than a dry autumn with a gradual decrease in temperature. Bodenheimer and Klein (1930) found that the ant, Messor semirufus was more resistant to heat in July than in March. Walshe (1948) showed that Chironomids collected from streams below 15°C had less resistance to heat than individuals taken from still water at 20°C.

Acclimatization to high or low temperatures has conditioning effects on the insect activity, its chill and heat-comas and mortality. Thus Calhoun (1954, 1960) found that Blatella germanica acclimatized at 15, 25 and 35°C had become active at minimum temperatures of 4, 5 and 7°C respectively. Mellanby (1954) pointed out that the activity of insects was limited at low temperatures by the chill-coma and at high temperatures by heat-coma point. The range could be altered readily by pre-exposure of the individuals to high or low temperatures. Using Tenebrio molitor he showed that insects acclimatized at 37°C could survive at 42°C while the ones adapted to 30°C died at 42°C. Calhoun (1954) examined the chill-coma of B. germanica acclimatized to 10 and 15°C and found it to be the same for the two temperatures. In view of this he concluded that there was a temperature for this species (15°C) below which further acclimatization did not take place.

Love and Whelchel (1957) tested the effect of high temperature on the immature stages of Anopheles quadrimaculatus and stated that mortality was affected by temperature, time of exposure and the rapidity with which temperature changed. Mortality was reduced when temperature was raised slowly; larvae suffered 50% death when temperature rose quickly to 37°C yet could survive a maximum of 42°C if the increase was gradual.

In the examples reviewed above, it was shown that insects subjected to high or low temperatures became adapted to tolerate higher or lower temperatures; their development, although checked, was completed. But Mellanby (1938) indicated that exposure of Lucilia sericata to high temperatures terminated the normal processes of development and led to diapause, thus rendering it resistant to high temperatures. He attributed this to the destruction, by high temperature, of hormones controlling the developmental processes. Wigglesworth (1952) recorded similar results with Rhodnius prolixus.

Baldwin (1954) drew the attention of other workers to the fact that acclimatization was not a simple case of rearing an insect under a high or low temperature to render it tolerant to higher and lower temperatures, because the determination of temperature tolerance was complicated by the age of the insect, the humidity and the thermal history. He gave an example of some insects reared at 17°C being more tolerant to higher temperature than ones reared at 23°C; the explanation was that more water was lost at 17°C during the longer developmental period at 17°C, the rate of loss of water at

17 and 23°C being the same.

Baldwin and House (1952, 1954) indicated that acclimatization to lethal high temperature was associated with an increase in the specific gravity and the osmotic pressure of the haemolymph. Their hypothesis suggested that a decrease in the percentage of water in the protoplasm of insects resulted in a higher tolerance to lethal high temperature. Mellanby (1934) demonstrated that exhaustion of food reserve was a factor contributing to death at high temperatures, but since starvation and the reduction of osmotic pressure of haemolymph go together (Wigglesworth, 1938) they lead to the same result.

Results presented by most of the mentioned authors indicate that the adaptation is reversible, but Simpson (1953) and Waddington (1953) suggested that environmentally acquired characters could somehow become genetically controlled. Simpson proposed three steps in acquisition:

(1) The appearance of new characters due to interaction with temperature.

(2) Occurrence of genetic factors which control the same acquired characters.

(3) The process of the spread of the genetic factor in the population.

(2) Effect of temperature on size.

The trends and magnitude of changes of the size of insects during the process of acclimatization has not received much attention. However, many observations have been made on the interaction between size and temperature. It is generally accepted that high temperatures reduce and low temperatures, within limitations, increase the size of insects. Titschack (1925, 1927) experimenting on Tineola biselliella at 30, 25, 20 and 15°C recorded the weight of the female insects to be 4.18, 5.06, 5.53 and 5.9 grms respectively. Uvarov (1931) explained the small size of insects at high temperatures to be due to a higher rate of development compared with relatively a slow uptake of food. Murdie (1965) quoted Imai (1933) as stating that "at low temperature, growth occurs slowly and more completely, while at high temperatures growth proceeds more rapidly and with less integrated completeness."

At temperatures near the lowest threshold for development, the size of insects is also reduced. In these conditions, although the rate of development is slow, perhaps the food uptake is slower or the food quality is poorer. A possible example of slow food uptake was presented by Burges and Cammell (1964) who reported that the weight of Trogoderma anthrenoides was reduced at temperatures near the lower and upper threshold for development.

Several workers on stored products pests have demonstrated that size was negatively correlated with temperature. Species

studied include Acanthoscelides obtectus (Menusan, 1936); Ephestia elutella (Waloff, Norris and Broadhead, 1948) and Sytophilus oryzae (Reddy, 1952). Similar results were reported on Diptera; Golightly and Lloyd (1939) and Golightly (1940) observed seasonal size variations of Psychoda spp.in the field under different larval crowding and temperature conditions and in the laboratory at different temperatures, and concluded that temperature was the most important single factor controlling the size of the species. Hosoi (1954) worked on Culex pipiens and showed that the larvae reared at high temperature developed into small adults.

Aphids have not received intensive quantitative study. Most of the authors who referred to the effect of temperature simply stated that they were "undersized", "small", "minute" or "degenerate" when reared at high temperatures and "bigger" or "heavier" at low temperatures. Rivny (1938) working on Toxoptera aurantii stated that the very small number of nymphs which survived at 30°C developed into small adults and died without reproducing. Aphis chloris reared at high temperature were smaller and yellower than normal ones (Wilson, 38). Kenton (1955) experimented on the effect of 29 - 30°C on Acyrthosiphon pisum and stated that the aphid showed abnormalities, the most important being the small size of the adult.

Bodenheimer and Swirski (1957) observed that the size of aphids collected in late winter were bigger than those collected in late summer, but they were not sure if this was the result of differing

nutritional conditions of the host or seasonal changes in the endocrine secretion in the insect induced by the different environmental conditions. Müller (1966) stated that the size of A. fabae increased with rise in temperature from 5°C and reached a maximum at 14 - 15°C after which it declined to reach its maximum size at 30°C.

Murdie (1965) reared Acyrthosiphon pisum at constant temperatures ranging from 10 to 28°C and showed that the size of the aphid followed this order of decrease in relation to temperature 15 > 10 > 20 > 25 > 28°C. At 25°C three generations were bred and their size decreased successively to the 3rd generation; when the adults of F_2 were transferred to 20°C, the size did not recover to the normal in the first generation, but approached the size of individuals kept at 20°C in the 2nd generation. Murdie also studied the size variation of other parts of the body and concluded that the proportional sizes of various characters varied within the different generations.

Husain et al (1944) working on Schistocerca gregaria reported that raising the temperature from 27 to 40°C reduced their weight, but more important that the relative proportions of the various parts were altered in a way which implied that high temperature induced the development of "gregaria" characters. Imai (1933) stated that the different parts of Drosophila sp. decreased at different rates under high temperatures; the femur was more stable than the wing length.

(3) Effect of temperature on reproduction.

Critically high and low temperatures reduce aphid fecundity. These temperatures vary from one species to another and also vary for the same species according to the thermal history of the individuals (p.138). Most earlier work centred on testing the effect of high or low temperatures on aphids' fecundity without pursuing this effect on the successive generations or seeing the trend of recovery when these insects were transferred to suitable temperatures. Rivny (1938) reported that Toxoptera aurantii deposited a few nymphs at 11°C and were sterile at 7°C. Temperatures above the optimum also reduced the number of progeny and at 33°C the aphid ceased to reproduce.

Lawson (1941) stated that high temperature (30°C) stopped reproduction in aphids in about 10 - 11 days; the first deposited nymphs matured while the ones born later died before becoming adults. Acyrthosiphon pisum reproduced about 32 nymphs at low temperature ranging from 5 to 9°C and the number of progeny increased with rise in temperature to 25°C. Any further rise in temperature was followed by a reduction in fecundity and the aphid ceased reproduction at 29 - 30°C. (Kenten, 1955). Lees (1959) working on Megoura viciae demonstrated that 25°C was near the upper limit for its continuous reproduction, and dissection of adults maturing at this temperature revealed a number of degenerating embryos. The maximum number of progeny was produced at 15 - 20°C, and although the adults often contained embryos,

reproduction ceased at 8°C. These adults when transferred to 20°C deposited about 4 nymphs each.

According to Barlow (1962) Macrosiphum euphorbiae deposited 34 nymphs at 5°C, reached a maximum at 10°C (50 nymphs) and then decreased to 14 at 25°C. At 30°C it failed to reproduce. Murdie (1965) studied the fecundity of Acyrthosiphon pisum at constant temperatures ranging from 10 to 28°C and recorded a minimum number of progeny at 28°C followed by 10°C. A number of generations were produced at 25°C and the progeny decreased steadily in the successive generations. Recovery when transferred to 20°C was quicker the smaller the number of generations at the high temperature.

(4) Effect of size on fecundity.

Literature reviewed under the previous subheadings indicated that size and fecundity were inversely related with high temperatures and also, within limits, with low temperatures. It follows that at optimum temperature the species attains its maximum size and fecundity, although this temperature is not necessarily the same for the two characters.

Fecundity is the number of nymphs deposited by a female throughout its life time, and although the absolute number may be high at the optimum temperature it is not the only criterion for a successful increase in the numbers of the aphid (p. 62). Fecundity can be assessed either by counting the number of nymphs deposited by the

female during its deposition period or by dissecting the ovaries to reveal the number of embryos. The latter method is not reliable and does not give a good estimation because at extreme temperatures some nymphs within the adults are not deposited (p. 76). Webber (1955) and ven den Heuvel (1963) working on Lucilia cuprina and Aedes aegypti respectively stated that the number of ovarioles depended on the size of adults. "True" fecundity was positively correlated with the size of Psychoda spp. (Golightly, 1940); Plutella maculipennis (Atwal, 1955); Cadra cautella (Tokahashi, 1956); Phytodecta olivacea and Phaedon cochleariae (Donia, 1958).

Murdie (1965) observed that although the size of A. pisum reared at high temperature was directly related to the fecundity, yet when the individuals at the high temperature were transferred to a temperature of 20°C, the recovery did not occur at the same rate for the two characters. In the 2nd generation the size approached the normal for the individuals constantly kept at 20°C, but the fecundity was quite low.

Developmental period is an important parameter in insect multiplication. All the research done on aphids in this respect has been based on results with the first generation at a particular temperature. Quantitative work on the developmental period for successive generations at critically high or low temperatures or on recovery when returned to favourable temperatures has not been attempted before with aphids.

C. MATERIALS AND METHODS.

First, the critically high temperature was determined. The first experiments were done at 29°C, but the population failed after one generation and most of the first generation individuals died during development. Two generations were bred at 28°C before the aphid failed so most of the work was done subsequently at 27.5°C.

The chosen critical low temperature was 10°C at which the rate of development of one generation was about 40 days so only two generations were bred. M. persicae reared at 20°C were used as controls.

The effects of temperature on size, fecundity, reproductive period and longevity of the aphid were tested at 10, 27.5, 28 and 29°C, but the effect on the development period only at 27.5°C. During all experiments the illumination was for 16 hours a day and the relative humidity ranged from 45 to 75%.

(1) Developmental period.

(a) The effect of 27.5°C on successive generations.

About 50 adult apterae reared under uncrowded conditions on brussels sprouts at 20°C were transferred to two small brussels plants. The adults were removed after 2 days when some nymphs had been deposited on each plant. The two plants were then placed in Watkins and Doncastor cages and transferred to 27.5°C constant temperature. Another set of experiments was concurrently done at the same temperature (27.5°C). 50 adults reared at 20°C were

transferred singly to mature leaf-discs of brussels sprouts floated on culture solution. Observations were made at 3 hours intervals and adults were removed when a single nymph had been deposited on each leaf-disc. Daily observations were made for about 5 days after which observations were made every 3 hours from 9 am. to 1 am. The times when the 4th exuvium was moulted and the first nymph deposited were recorded. All the adults with their progeny from this experiment were discarded.

Moulting and deposition of the nymph were assumed to have occurred mid-way between the observation and the one before it. The time from birth to the 4th moult and from the latter to the deposition of the first nymph are the developmental and the pre-larviposition periods respectively for the first generation (F_1).

When the nymphs on the brussels sprout plants of the first experiment had completed development, about 30 of the young adults were then transferred singly to leaf-discs floating on culture solution and the same procedure adopted as described above to obtain the developmental duration and the pre-larviposition period for F_2. The rest of the adults on the brussels sprouts were transferred to two fresh plants and kept for two days before they were removed. Their progeny matured on the plant and when the adults appeared, some of them were transferred to leaf-discs and the rest to fresh plants. Thus the cultures of the different generations were maintained on the brussels sprouts and the rates of development for each generation

were examined on the leaf-discs from each generation. Examination of the developmental period was done on leaf-discs, because observations took a short time and the results were more accurate than on the plants. Nine generations were bred at this temperature.

(b) Recovery at 20°C.

Some adults from F_4 and F_9 generations at 27.5°C were transferred to brussels sprout leaf-discs and kept at 20°C. Results for 4 and 5 successive generations respectively at this temperature were collected to assess the trend of changes in the developmental period. The procedure for breeding the different generations on brussels sprouts and recording durations of development on leaf-discs for each generation was as described above.

2. Size and fecundity.

(a) Fecundity at 27.5°C and recovery at 20°C after each generation.

At 20°C a culture of M. persicae was kept on brussels sprouts for one year. Adult apterae, from this culture, reared in uncrowded conditions were transferred to two small brussels sprout plants, and removed after two days. The two plants, bearing the progeny of these adults were placed in Watkins and Doncaster cages and transferred to 27.5°C. When these had completed development, 60 young adults were transferred singly to mature leaf-discs of brussels sprouts floated on culture solution. 30 of these adults were kept

at 27.5°C and the rest were returned to 20°C. Observations were made twice daily when nymphs deposited were counted and removed until death of the adults. The fecundity of the first generation (F_1) was thus obtained. The tubes and the plastic boxes were topped up with the culture solution and water respectively every second day. The leaf-discs were replaced once a week.

The rest of the adults on the brussels sprouts were transferred to two fresh plants and kept for two days after which they were removed and taken to the laboratory for measurement. Their progeny, on the plants, were kept at 27.5°C and when the nymphs attained maturity, 40 newly emerging adults were transferred to leaf-discs on culture solution; 20 of these were kept at 27.5°C and the rest were transferred to 20°C and the fecundity of F_2 generation was examined as described above. The rest of the adults from the F_2 generation were transferred to two fresh plants for 2 days and then collected and taken to the laboratory to assess the effect of temperature on the adult size of the second generation (F_2). The effect of 27.5°C on five generations and their recovery at 20°C, after each generation, was examined.

(b) Recovery after transfer to 20°C.

About 10 adults of the 4th generation reared and kept at 27.5°C, as explained above, were transferred to a brussels sprout plant and taken to the 20°C room and kept overnight. Then the adults were discarded and the progeny left to develop. When the nymphs matured,

the fecundity of the first generation (F_4/F_1) was tested at this temperature only. The remaining first generation F_4/F_1 adults were transferred to a fresh plant and then removed on the second day for measuring. The progeny was kept at 20°C. Three successive generations (F_4/F_1, F_4/F_2, F_4/F_3) were bred at this temperature to determine the trends of fecundity and size recovery.

(c) The effect of other temperatures.

At 10, 28 and 29°C the same procdure for 27.5°C was adopted to determine the effect on size, fecundity, reproductive period and longevity and their recovery when returned to 20°C after each generation. 2, 2 and one generations respectively were reared at 10, 28 and 29°C.

Adult body length, fecundity, reproductive period and longevity were determined in successive generations kept at 20°C. The results of the two generations at the same temperature showed almost the same pattern (tables 22 and 23). The results obtained at 20°C in this section and also in section II (table 11) suggested that there would be no significant effects.

3. Size measuring.

Adults reared at the various temperatures and conditions were prepared and mounted as already described (p. 10). The lengths and the width of the body, the lengths of the siphunculi, the cauda, the hind tibia and the 3rd, 4th, 5th and the 6th antennal segments

(the total of these being referred to as the antenna) were measured using a monocular microscope as described on page 11. The length of these appendages on the right and left sides of the aphid not being isometric, all the measurements were restricted to the right side.

D. RESULTS.

(I) Development.

Summary of the developmental, pre-larviposition and adult maturation periods for the nine generations reared at 27.5°C, and analysis of the data are presented in tables 16 and 17 respectively.

Table 16. Mean values of developmental, pre-larviposition and maturation periods (hours).

Generation	No. of aphids	Developmental period of larva	Pre-larviposition period	Maturation period of adult
F_1	9	135.5	14.4	150.0
F_2	26	133.9	15.0	149.0
F_3	15	131.6	19.5	151.1
F_4	21	138.4	16.2	154.7
F_5	22	137.8	14.1	152.0
F_6	8	136.6	16.6	153.3
F_7	8	133.8	16.3	150.2
F_8	13	138.4	15.9	154.3
F_9	14	134.6	16.5	151.2

The F_1 generation showed a marked decrease in developmental and pre-larviposition periods compared with the corresponding figures at 20°C which were 182.9 and 17.3 hours respectively. The former also decreased in the 2 succeeding generations (F_2 and F_3), but the

following generations did not exhibit a clear pattern; comparatively longer durations being followed by shorter ones. The discrepancies in duration between the different generations were small and were only significant between F_3 compared with F_4 and F_8 at $p < 0.05$. Analysis by 't' test (table 17) illustrated that the durations of all 9 generations were significantly shorter than at 20°C at $p < 0.001$.

The parturition and maturation periods did not show any pattern, and the differences between those of the various generations at the same temperature were small and did not reach significance at $p < 0.05$. The pre-larviposition period at 27.5°C was shorter than at 20°C for all the generations except F_3 which was longer. Table 17 shows that all maturation periods were shorter than at 20°C.

Table 17. Summary of comparisons between the means at 27.5 and 20°C.

Generation	Developmental period		Maturation period	
	Difference of means (hours)	significance	Difference of means (hours)	significance
F_1	47.4	***	50.2	***
F_2	49.0	"	51.2	"
F_3	51.3	"	49.1	"
F_4	44.5	"	45.5	"
F_5	45.1	"	48.2	"
F_6	46.3	"	46.9	"
F_7	49.1	"	50.0	"
F_8	44.5	"	45.9	"
F_9	48.3	"	49.0	"

Recovery at 20°C.

F_4 and F_9 adults reared and kept at 27.5°C were returned to 20°C and reared for 4 and 5 generations respectively. Tables 18 and 19 show the means of developmental, pre-larviposition and maturation periods. The developmental periods of F_4/F_1 and F_9/F_1 generations at 20°C were longer than when kept constantly at 20°C. The period decreased in successive generations and became shorter than for individuals kept constantly at 20°C. This decrease was most remarkable with aphids exposed longest to the high temperature (table 19).

Table 18. Mean values of developmental, pre-larviposition and maturation periods of individuals kept at 20°C after 4 generations at 27.5°C (hours).

Generations at 20°C	Nol of aphids	Developmental period of larva	Pre-larviposition period	Maturation period of adult
F_1	21	189.5	16.6	206.1
F_2	25	184.5	12.9	197.5
F_3	23	181.1	16.9	198.2
F_4	21	173.0	16.6	189.6

Table 19. Mean values of developmental, pre-larviposition and maturation periods of individuals kept at 20°C after 9 generations at 27.5°C (hours).

Generations at 20°C	No. of aphids	Developmental period of larva	Pre-larviposition period	Maturation period of adult
F_1	27	185.2	17.5	202.7
F_2	22	173.1	13.1	186.3
F_3	30	156.9	14.5	171.5
F_4	30	151.1	17.5	168.6
F_5	34	163.5	14.4	177.9

Tables 20 and 21 present an analysis of significance between the mean durations of individuals returned to 20°C after 4 and 9 generations respectively, also a comparison of these means with those of the individuals continuously reared at 20°C (182.9 hours). The figures in parenthesis are the differences between two means.

Table 20. Test of significance of mean differences.

	F_4/F_1	F_4/F_2	F_4/F_3	F_4/F_4	At 20°C
At 20°C	(+6.6)NS	(+1.6)NS	(-1.8)NS	(-9.9)NS	0
F_4/F_4	(+16.5)***	(+11.5)**	(+8.1)***	0	
F_4/F_3	(+8.4)***	(+3.4)NS	0		
F_4/F_2	(+5.0)NS	0			
F_4/F_1	0				

N.S. - not significant; * - $p < 0.05$; ** - $p < 0.01$; *** - $p < 0.001$

Table 21. Test of significance of mean differences.

	F_9/F_1	F_9/F_2	F_9/F_3	F_9/F_4	F_9/F_5	At 20°C
At 20°C	(±2.3)NS	(-9.1)NS	(-26.0)***	(-31.8)***	(-19.4)**	0
F_9/F_5	(+21.7)***	(+9.6)***	(-6.6)***	(-12.4)***	0	
F_9/F_4	(+34.1)***	(+22.0)***	(+5.8)***	0		
F_9/F_3	(+28.3)***	(+16.2)***	0			
F_9/F_2	(+12.1)***	0				
F_9/F_1	0					

NS - not significant; * - $p < 0.05$; ** - $p < 0.01$; *** - $p < 0.001$

(2) Effect of temperature on fecundity, reproductive period and longevity.

A summary of the results is given in table 22 and some detailed observations on the pattern of daily reproduction at the various temperature treatments are presented in figs. 10 to 21.

(a) Effect of temperature on fecundity.

(i) Effect of 10°C. Two successive generations were reared at 10°C; the fecundity of some adults of these generations was examined at 20°C. The mean numbers of progeny per adult decreased from 19.4 in the first generation to 5.6 in the second. The adults of F_1 and F_2 generations reared at 10°C and then returned to 20°C produced almost the same number of progeny (table 22) but at 10°C continuously the fecundity was much decreased. Detailed reproduction rates are shown in figs. 10 and 11.

Table 22. Summary of the mean fecundity, reproductive period and longevity at the various temperatures.

Rearing Temp.	Generation	Temp. at which fecundity tested	No. of aphids	Fecundity	Reproductive period (days)	Longevity (days)
10°C	F_1	10°C	18	19.4	14.6	18.7
		20°C	16	33.5	8.1	9.5
	F_2	10°C	13	5.6	5.8	13.5
		20°C	15	34.7	9.2	11.5
20°C	F_1	20°C	24	39.7	10.5	13.0
	F_2	20°C	22	38.5	9.9	12.3
27.5°C	F_1	27.5°C	30	33.5	8.9	12.2
		20°C	28	14.0	6.6	9.3
	F_2	27.5°C	18	20.8	7.4	9.5
		20°C	17	19.8	10.2	13.6
	F_3	27.5°C	12	8.8	3.6	5.5
		20°C	12	19.5	9.2	12.0
	F_4	27.5°C	12	5.9	3.4	5.3
		20°C	12	22.0	13.2	15.8
	F_5	27.5°C	5	1.8	1.2	3.4
		20°C	6	16.8	10.5	13.0
4 generations at 27.5°C						
+1 at 20°C	F_4/F_1	20°C	18	27.3	8.5	13.2
+2 " "	F_4/F_2	20°C	26	27.1	7.4	11.0
+3 " "	F_4/F_3	20°C	22	34.2	8.1	11.8
28°C	F_1	28°C	29	20.2	9.4	11.0
		20°C	27	17.9	9.8	12.5
	F_2	28°C	23	15.6	5.8	7.9
		20°C	17	14.8	8.5	11.5
29°C	F_1	29°C	41	22.2	6.5	8.5
		20°C	28	18.1	9.2	12.0

Fig. 10. Mean daily number of progeny produced by apterous virginoparae *M. persicae* reared for two successive generations at 10°C. Fecundity examined at 10°C (O), at 20°C (X) and constantly kept at 20°C (Δ).

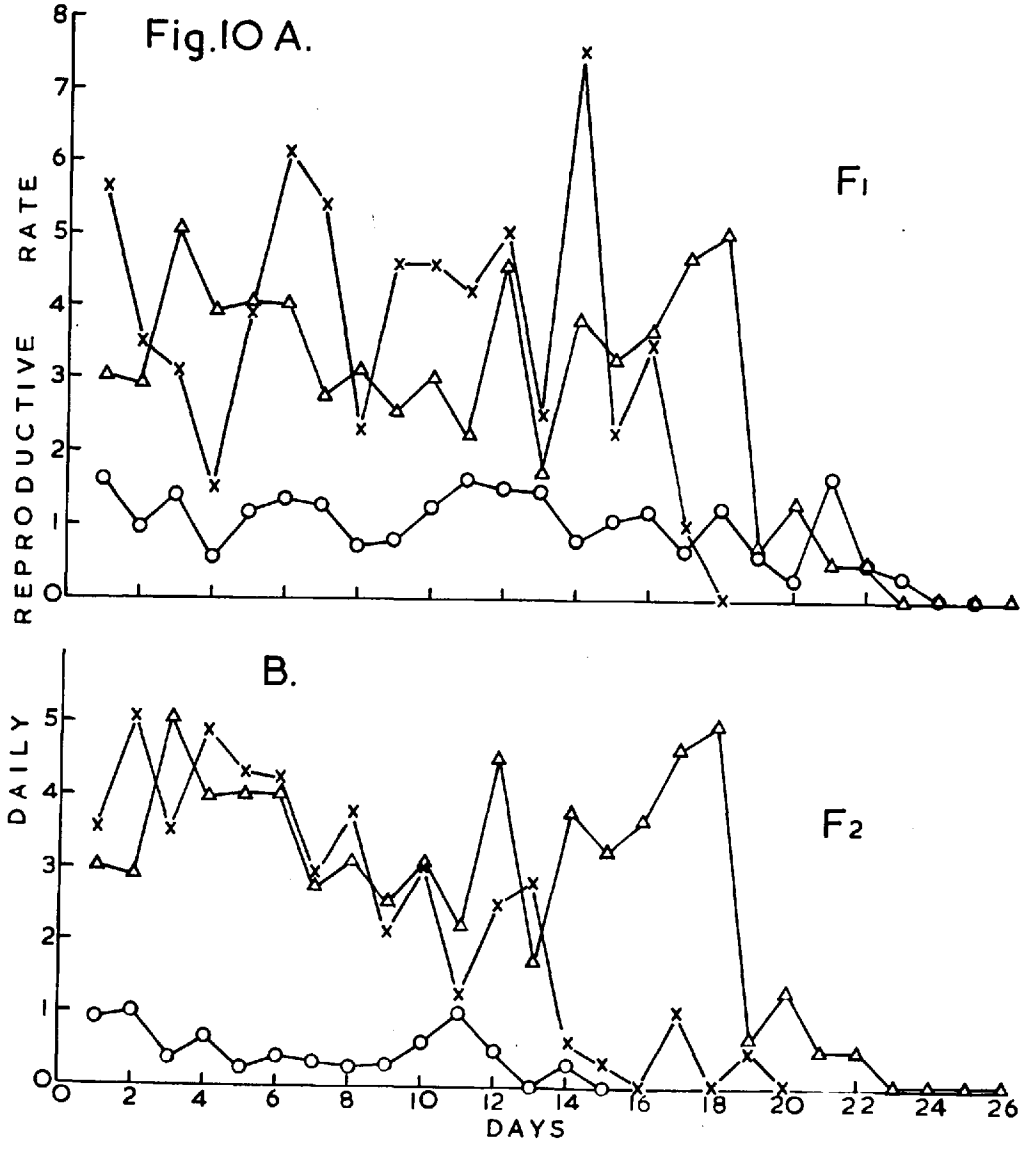


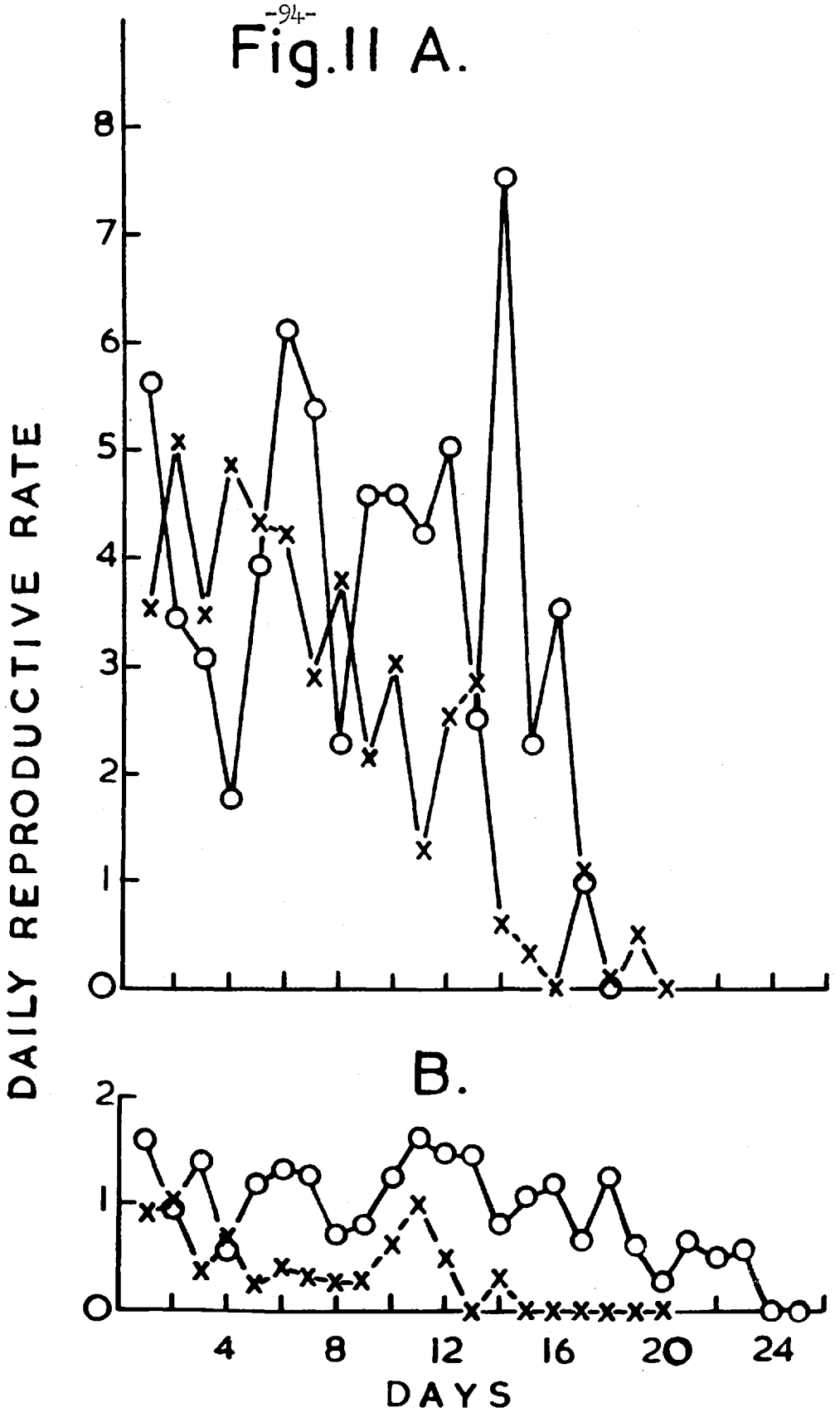
Fig.10 A.
REPRODUCTIVE RATE
F1
B.
DAILY
F2
DAYS
0
1
2
3
4
5
6
7
8
2
4
6
8
10
12
14
16
18
20
22
24
26

Fig. 11. Daily rate of reproduction of two successive generations of *M. persicae* reared at 10°C.

A. Fecundity of F_1 (0) and F_2 (X) examined at 20°C.

B. Fecundity of F_1 (0) and F_2 (X) examined at 10°C.

Fig.11 A.



The pattern of daily reproduction of F_1 and F_2 aphids returned as adults to 20°C was different (figs. 10A and B, and 11A). The F_1 daily reproduction was remarkably high on the first, 6th and 14th days of the transfer. Such rates were not attained by adults constantly reared at 20°C at any time of their reproductive life. The daily reproductive rate of the F_2 adults did not exceed the daily maximum of those kept continuously at 20°C.

(ii) Effects of 27.5°C. The mean fecundities per adult of aphids reared continuously at 27.5°C were 33.5, 20.8, 8.8, 5.9 and 1.8 for the first, second, third, fourth and the fifth generations respectively, the decrease in F_1, F_2 and F_3 generations was significant at $p = < 0.05$. The individuals reared at 27.5°C and then kept at 20°C when adult produced 14.0, 19.8, 19.5, 22.0 and 16.8 progeny per adult for F_1, F_2, F_3, F_4 and F_5 generations respectively i.e. about half of those produced by adults kept continuously at 20°C. It is noticeable that the F_1 adults produced relatively few progeny.

Fig. 15 shows that the differences in daily reproductive rates between adults of F_1 at 27.5°C and adults returned to 20°C were remarkable. The former produced more in the first 10 days, but in the last few days of the reproductive period the adults returned to 20°C produced more. These differences in the early daily reproductive rates of F_2, F_3 and F_4 adults became smaller in the successive generations and in the F_5 generation showed the opposite trend

Fig. 12 - 14. Mean fecundity, reproductive period and longevity of *M. persicae* reared for a number of generations at various temperature treatments.

Reared and examined at 27.5°C (0);

reared at 27.5°C and examined at 20°C (X);

returned after 4th generation at 27.5°C

and reared at 20°C for 3 generations (●);

reared and kept constantly at 20°C (△)

Fig.12.

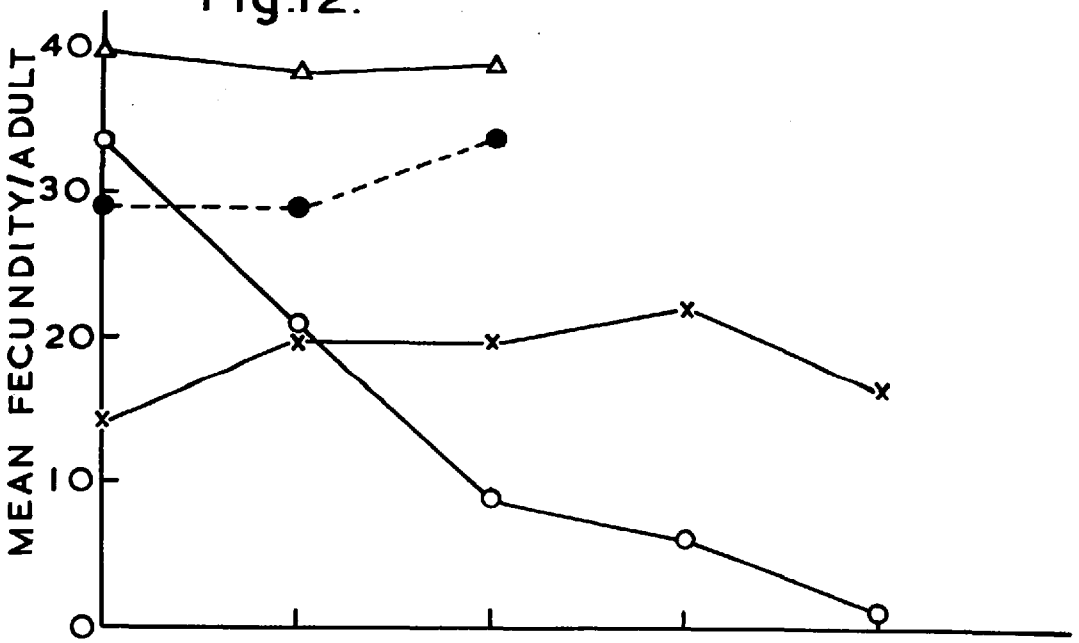


Fig.13.

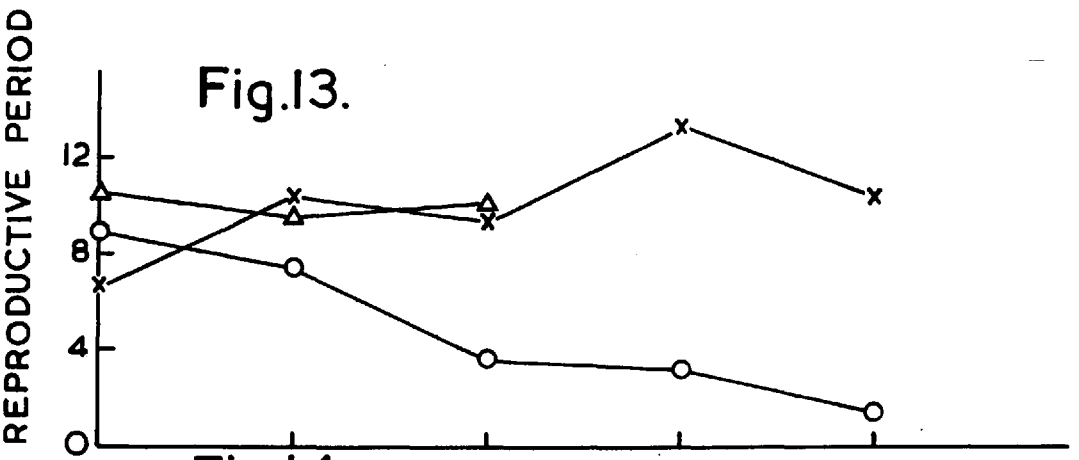
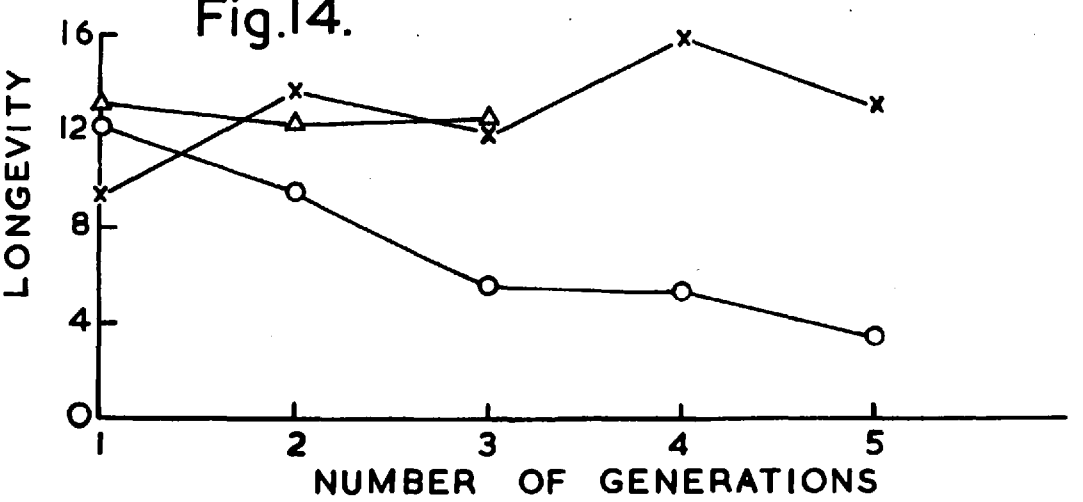


Fig.14.



i.e. adults returned to 20°C produced more progeny in the first 3 days (fig. 19).

(iii) Recovery at 20°C. Some adults of the F_4 generation at 27.5°C were returned to 20°C and the fecundity of aphids of the three following generations reared throughout at this temperature were 27.2, 27.1 and 34.2 respectively. The fecundities of the first two generations were the same, while there was an increase in the third. However, the value for the 3rd generation was still smaller than that of aphids kept constantly at 20°C, (table 22 and fig. 12). The pattern of reproduction of these recovering adults is presented in fig. 20. The reproduction rate of F_1 adults was suppressed for the first 8 days and then reached a maximum on the 10th day, which was greater than the maximum attained by aphids reared continuously at 20°C. The reproductive rate of F_2 and F_3 adults rose successively in the early days of reproduction and then followed almost the same trend as F_1 adults for the rest of their reproductive lives.

Individuals reared at 28°C produced 20.2 and 15.6 nymphs/adult for the first and second generations respectively. F_1 adults returned to 20°C produced 17.9 which was less than the fecundity of F_1 at 28°C. F_2 adults deposited almost equal numbers at 28 and 20°C (table 22).

Adults of the F_1 generation reared at 29°C showed the same trend as at 28°C by producing less progeny when returned as adults to 20°C. Fig. 21 shows that the daily reproductive rate of adults

Figs. 15 - 19. Daily rate of reproduction of apterous virginoparae *M. persicae* reared at 27.5°C for 5 generations.
Fecundity examined at 27.5°C (O);
Fecundity examined at 20°C after each generation (●);
Reared and kept constantly at 20°C (X).

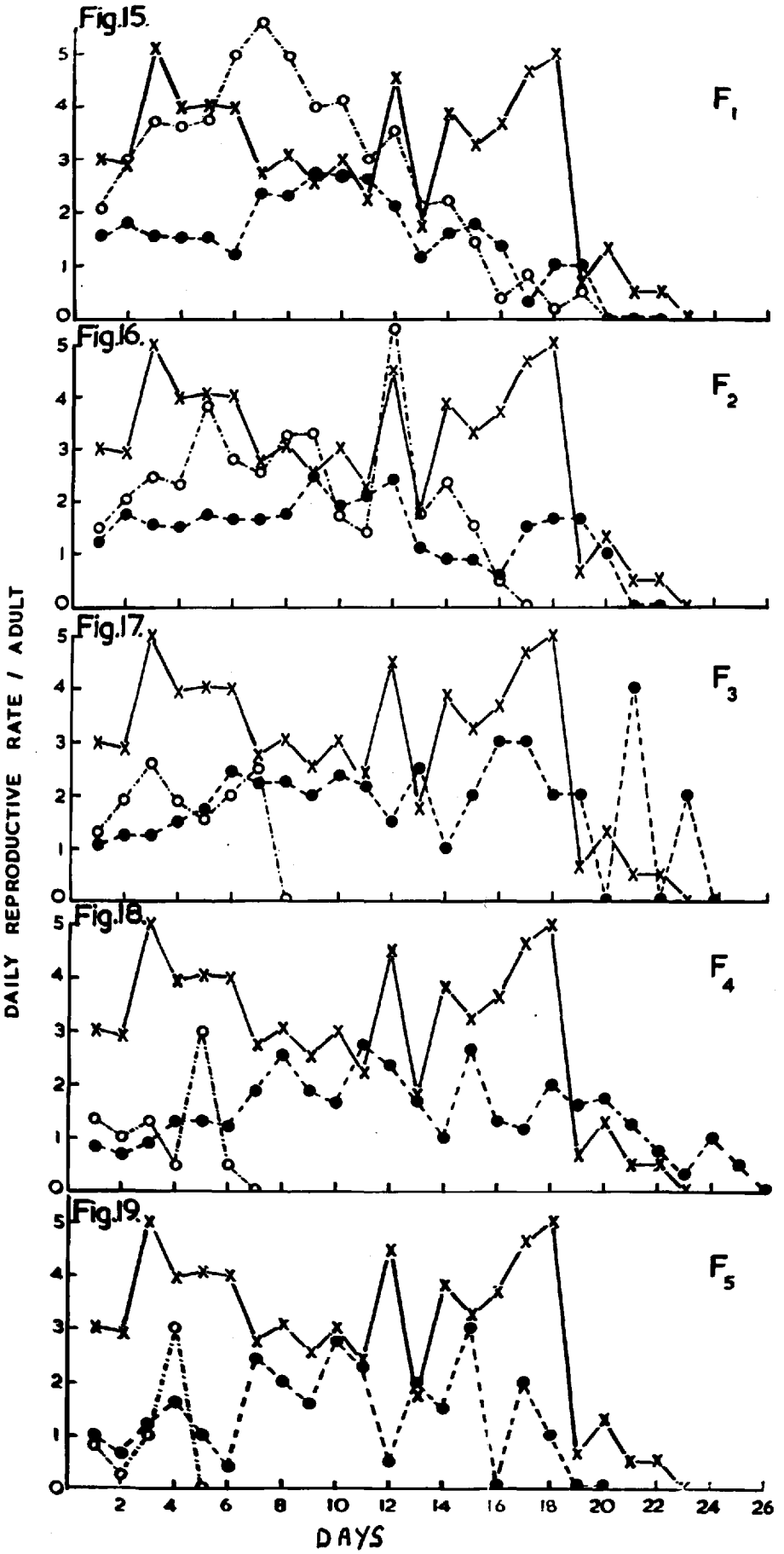


Fig.15.
F1
Fig.16.
F2
Fig.17.
F3
Fig.18.
F4
Fig.19.
F5
DAILY REPRODUCTIVE RATE / ADULT
0
1
2
3
4
5
2
4
6
8
10
12
14
16
18
20
22
24
26
DAYS

Fig. 20. Daily rate of reproduction of 3 successive generations of *M. persicae* returned to 20°C after 4 generations at 27.5°C.

Fig. 20.

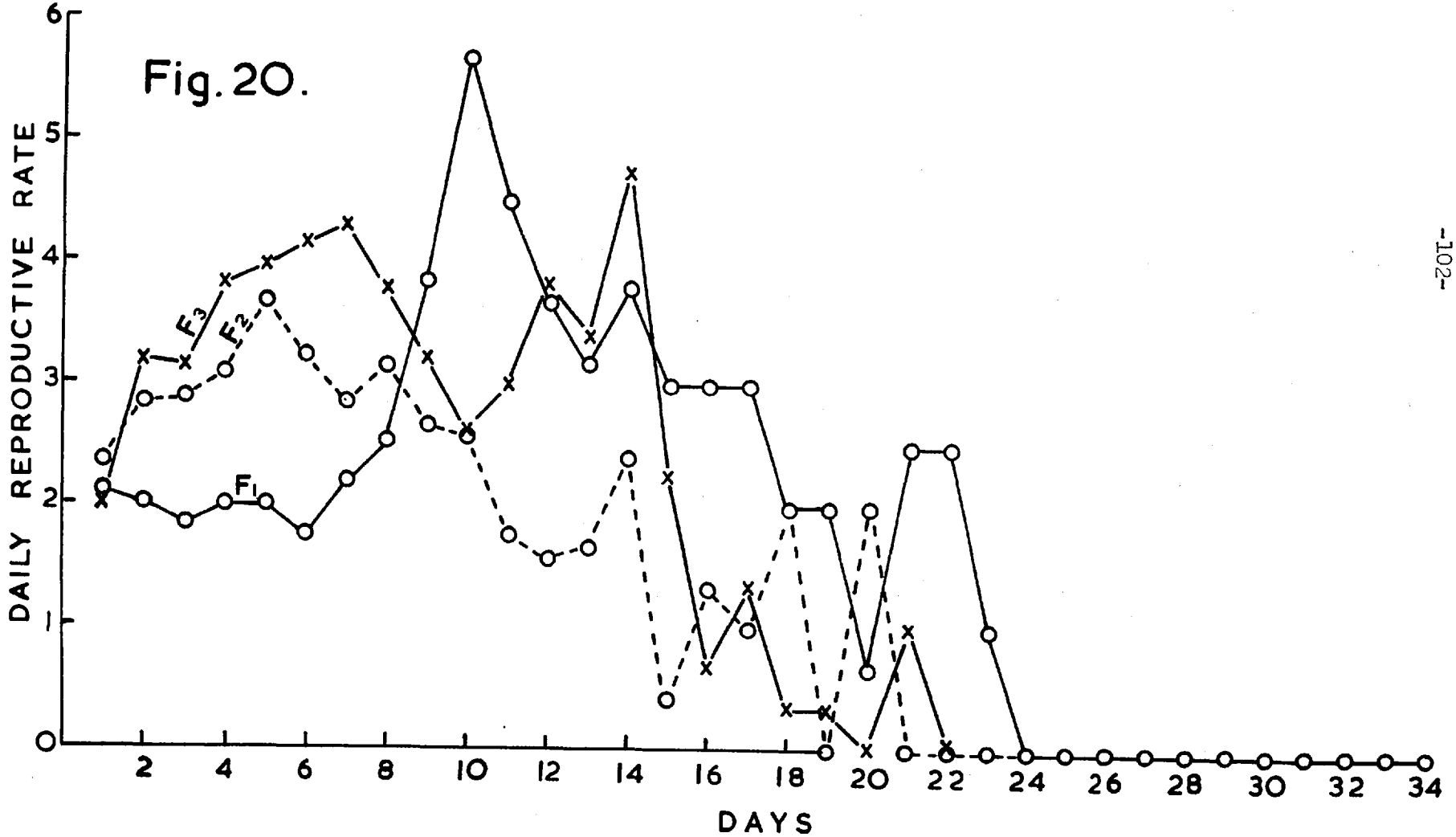

DAILY REPRODUCTIVE RATE
0
1
2
3
4
5
6
F1
F2
F3
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
DAYS

Fig. 21. Daily rate of reproduction of M. persicae reared for one generation at 29°C.

Fecundity examined at 29°C (0); at 20°C (x) and constantly kept at 20°C (Δ).

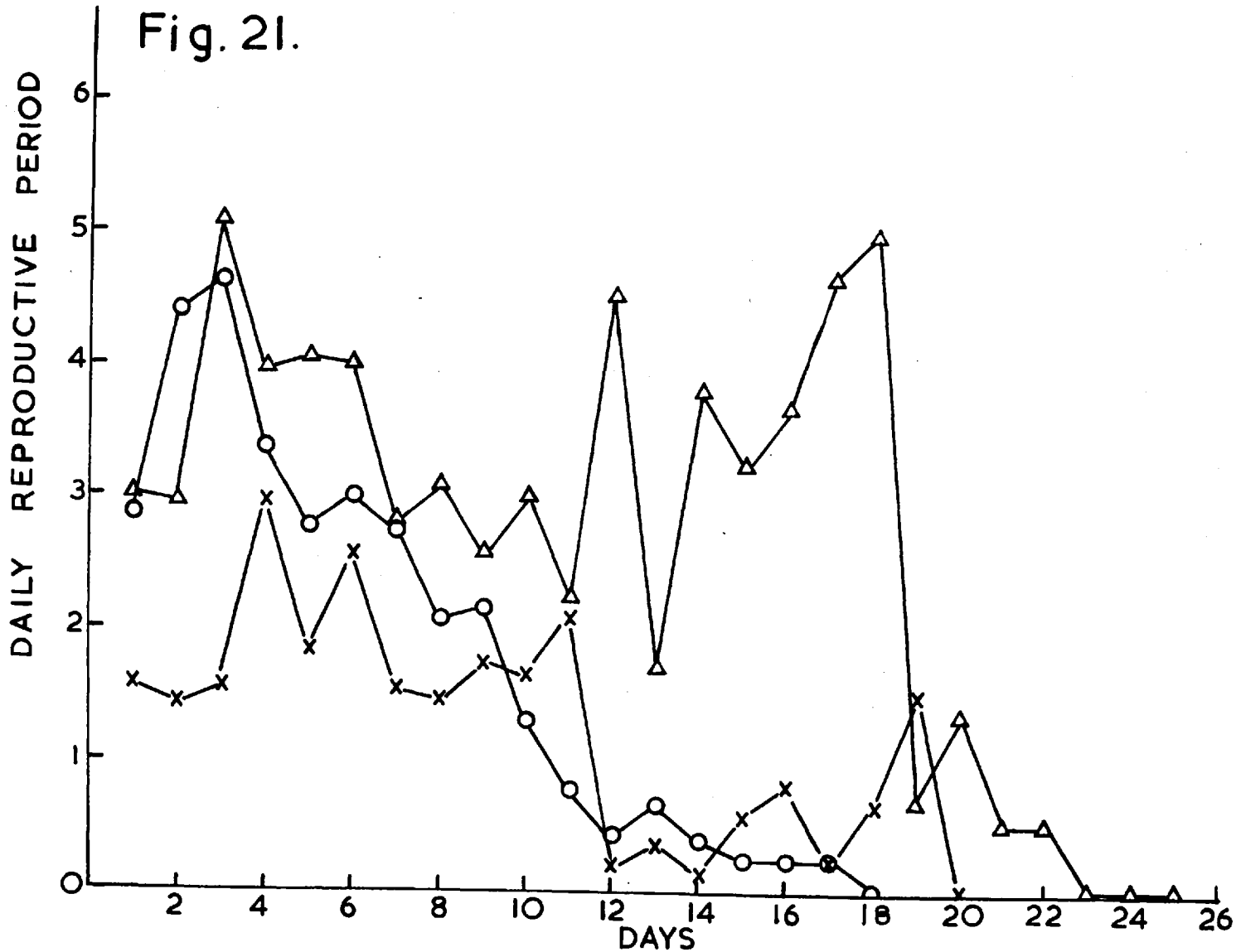


Fig. 21.
DAILY REPRODUCTIVE PERIOD
0
1
2
3
4
5
6
2
4
6
8
10
12
14
16
18
20
22
24
26
DAYS

returned to 20°C were noticeably lower in the first 9 days compared with those kept at 29°C and also with individuals kept constantly at 20°C. However, in the last days of reproduction, the daily rates were higher than at 29°C.

(b) Effect on reproductive period.

At 10°C the reproductive period decreased from 14.6 days in the first generation to 5.8 days in the second. It was almost equal in F_1 and F_2 generations returned to 20°C. At 27.5°C it decreased from 8.9 days in the first generation to 1.2 in the 5th generation (table 22 and fig. 13). F_1 adults returned to 20°C reproduced for the shortest period (6.6) compared with 10.2, 9.2, 13.2 and 10.5 for F_2, F_3, F_4 and F_5 generation respectively.

The reproductive period for the individuals returned to 20°C and reared for 3 generations were 8.5, 7.1 and 8.1 days for the 1st, 2nd and 3rd generations respectively; these were slightly shorter than the figures for individuals continuously reared at 20°C. At 28°C the reproductive period decreased from 9.4 days to 5.8 days in the second generation, following the same trend as at 27.5°C, but the reproductive period for F_1 adults transferred from 28°C to 20°C was almost equal to that of the 1st generation, the fecundity of which was examined at 28°C. At 29°C adults transferred to 20°C reproduced for a longer period in the F_1 generation than those kept at 29°C (table 22).

(c) Effect on longevity.

At 10°C F_1 and F_2 adults lived longer than the individuals returned to 20°C. Longevities at 27.5, 28 and 29°C followed the same trends as the reproductive periods (table 22 and fig. 14).

(3) Effect of temperature on size.

(a) Effect of 10°C.

A summary of the mean lengths of various body parts of adult apterae reared at the different temperatures is presented in table 23. The lengths of the various parts for the 2 and 5 generations reared at 10°C and 27.5°C respectively and also the trends of the changes for 3 generations when transferred from 27.5 to 20°C are shown in fig. 22. The body length and width of the adults of F_1 generation reared at 10°C were greater than the corresponding parts of those reared at 20°C; the other parts, except the 3rd antennal segment and the cornicle were also slightly longer. The body length and width of the F_2 generation showed a further increase, but the other parts were shorter.

(b) Effect of 27.5, 28 and 29°C.

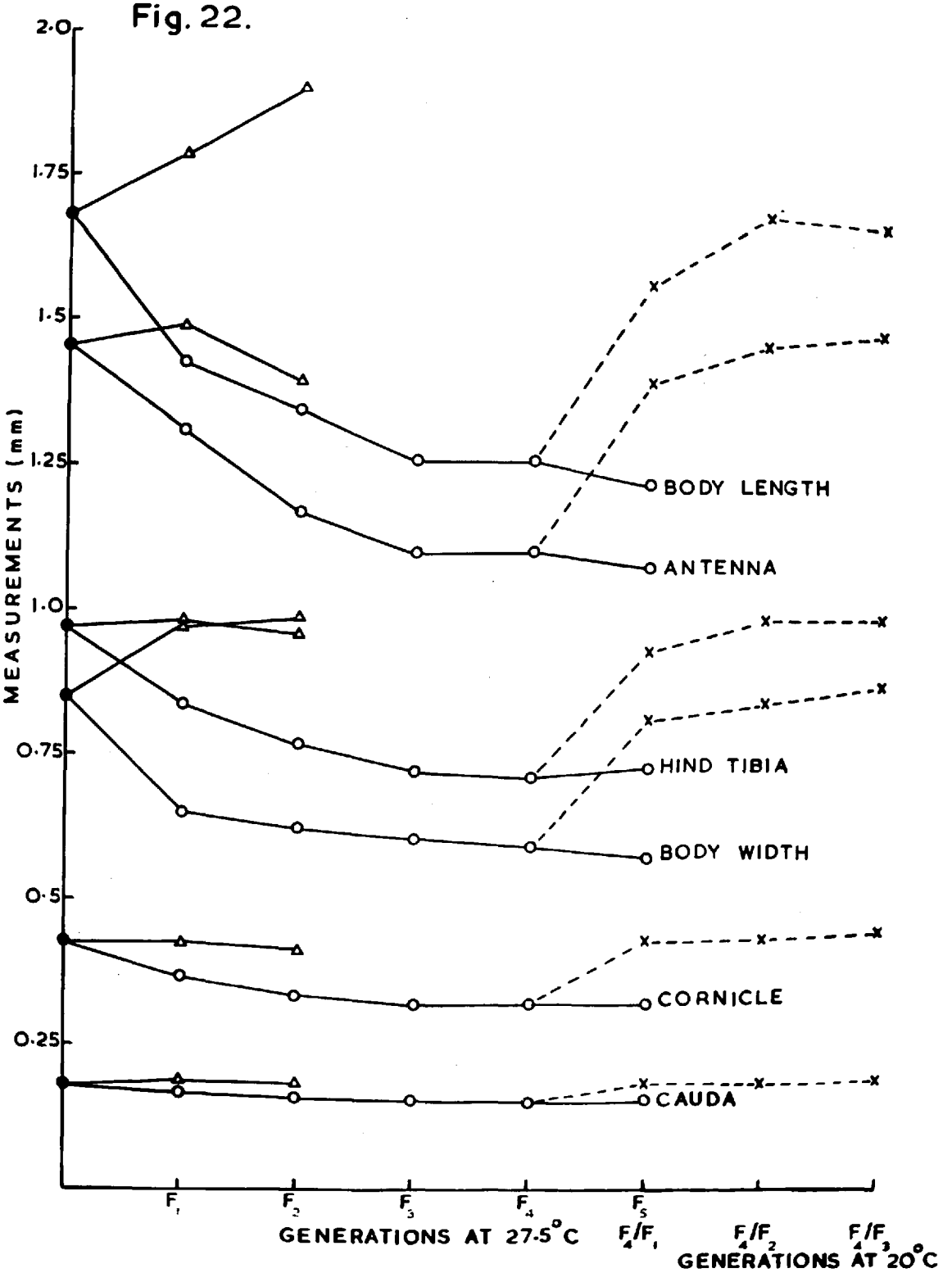
The body parts of F_1 adults reared at 27.5, 28 and 29°C were shorter than the corresponding ones at 20°C, but they did not show the expected trend of being shortest at the highest temperature (table 23) i.e. the body length and width were shorter at 27.5°C than

Table 23. Summary of the mean sizes (μ) of the various parts of adult apterous M. persicae reared at different temperatures.

Temp.	Generation	Length	Width	Antennal segments 3	4	5	Base	Unguis	6	Total	Cornicle	Cauda	Tibia 3
10°C	F_1	1782.5	969.2	380.1	301.6	244.4	119.4	442.6	562.0	1488.3	424.3	184.1	978.6
	F_2	1899.7	984.3	352.9	301.5	234.4	126.3	375.9	502.3	1391.1	413.9	180.5	959.2
20°C	F_1	1656.5	801.9	383.3	288.5	232.5	117.4	421.0	538.4	1442.7	424.4	176.6	958.8
	F_2	1682.3	840.7	384.9	291.0	235.2	117.3	421.9	539.2	1463.4	425.1	179.4	980.1
27.5°C	F_1	1422.5	651.2	347.9	254.9	197.2	107.2	399.6	506.8	1306.8	368.6	165.1	836.9
	F_2	1340.0	622.4	312.1	221.5	174.8	102.4	356.6	459.0	1167.6	337.8	158.9	767.4
	F_3	1256.0	605.0	294.0	202.6	159.5	98.6	344.5	443.2	1099.5	317.0	151.4	720.7
	F_4	1256.0	593.0	292.4	202.6	159.4	98.5	346.8	445.4	1100.0	321.1	148.1	710.2
	F_5	1215.3	373.7	291.6	194.2	157.9	100.3	327.8	428.2	1072.0	321.9	152.2	727.1
4 generations at 27.5°C +1 at													
20°C	F_4/F_1	1610.7	809.5	382.8	273.4	218.6	116.5	399.8	516.3	1391.1	426.8	183.5	930.7
+2 "	F_4/F_2	1677.9	839.4	392.1	293.5	231.5	115.5	417.3	532.8	1450.0	432.0	181.6	983.1
+3 "	F_4/F_3	1661.3	868.9	397.1	294.3	233.1	117.2	426.5	543.7	1468.1	440.9	186.4	982.7
28°C	F_1	1486.4	760.2	380.1	271.0	210.9	114.1	411.2	525.4	1387.2	394.4	178.7	915.1
	F_2	1388.8	693.9	322.2	226.1	170.4	97.6	370.4	468.2	1187.1	342.5	162.0	797.1
29°C	F_1	1474.6	719.2	349.9	253.9	197.2	105.4	379.8	485.2	1286.3	371.6	163.3	875.0

Fig. 22. The mean lengths of the different parts of M. persicae adult reared for 2 successive generations at 10°C (△), 5 successive generations at 27.5°C (0), recovery at 20°C after 4 generations at 27.5°C (X) and continuously kept at 20°C (●).

Fig. 22.


2·0
1·75
1·5
1·25
1·0
0·75
0·5
0·25
MEASUREMENTS (mm)
BODY LENGTH
ANTENNA
HIND TIBIA
BODY WIDTH
CORNICLE
CAUDA
F1
F2
F3
F4
F5
GENERATIONS AT 27·5°C
F4/F1
F4/F2
F4/F3
GENERATIONS AT 20°C

at 28 and 29°C. Body parts of F_2 adults reared at 27.5°C and 28°C were shorter than those of the F_1 at the same temperatures; at 27.5°C those of the F_3 were even shorter, but the body parts in F_4 were almost equal to those of the F_3. However, the body length and width and the length of the 6th antennal segment decreased slightly in the F_5 generation.

(c) Recovery at 20°C.

When adults of the F_4 generation, reared at 27.5°C, were transferred to 20°C, the various parts of the F_1 progeny were longer than those of the F_1 at 27,5°C, but still shorter than the corresponding parts of the individuals continuously reared at 20°C. However, the length of the different parts of F_4/F_2 generation approached those of the adults at 20°C (table 23 and fig. 22). The parts of the F_4/F_3 generation were almost equal to those of F_4/F_2 generation except for the body width and cauda.

Correlation coefficients were calculated to examine interrelationships between the various parts at 10°C and 27.5°C. Tables 24 and 25 present correlations of the characters in the first generation at 10°C and 27.5°C respectively. Clearly there was positive correlations between the characters at the two temperatures, but they differed in magnitude; correlations being remarkably lower at 10°C. At this temperature the best correlation was between the 6th antennal segment and hind tibia ($r = 0.719$) followed by the correlation between the 3rd antennal segment and tibia 3 ($r = 0.675$).

Table 24. Correlation coefficients for 8 characters of M. persicae reared for one generation at 10°C.

		Body length	Antennal segments 3	4	5	6	Cornicle	Cauda	Tibia 3
Tibia 3		0.554	0.675	0.653	0.536	0.719	0.159	0.229	1
Cauda		0.520	0.228	0.492	0.353	0.249	0.519	1	
Cornicle		0.619	0.249	0.075	0.110	0.039	1		
Antennal segments	6	0.177	0.399	0.459	0.588	1			
	5	0.237	0.257	0.299	1				
	4	0.436	0.492	1					
	3	0.558	1						
Body length		1							

The poorest correlation was between the 6th antennal segment and the cornicle (r = 0.039). The values for the 1st generation at 27.5°C were comparatively greater than those at 10°C. There was a high positive correlation between tibia 3 and the 3rd antennal segment (r = 0.929) and also the tibia and the 4th antennal segment (r = 0.906). As at 10°C the poorest correlation was between the lengths of the 6th antennal segment and the cornicle (r = 0.453), but it was better than at 10°C.

Significant differences in correlations being experienced in F_1 generation at both temperatures, the coefficients for F_2 at 27.5°C were calculated (table 25). Clearly there was a marked increase in correlation coefficients for all the characters examined.

Table 25. Correlation coefficients for 8 characters of M. persicae reared for one generation at 27.5°C.

		Body length	Antennal segments 3	4	5	6	Cornicle	Cauda	Tibia 3
Tibia 3		0.832	0.929	0.906	0.848	0.723	0.755	0.773	1
Cauda		0.721	0.705	0.698	0.548	0.492	0.781	1	
Cornicle		0.859	0.764	0.666	0.504	0.453	1		
Antennal segments	6	0.562	0.767	0.769	0.815	1			
	5	0.570	0.832	0.897	1				
	4	0.721	0.877	1					
	3	0.829	1						
Body length		1							

These were particularly high between the tibia 3 and the following characters :- 3rd antennal segment (r = 0.961), the cornicle (r = 0.953), the body length (r = 0.935) and the 4th antennal segment (r = 0.911). Also the body length with the cornicle (r = 0.944) and the 3rd antennal segment (r = 0.934). The poorest correlation was between the length of the 6th antennal segment and that of the cauda (r = 0.534), followed by the 5th segment with the cauda (r = 0.540).

Correlation coefficients between the body length and seven other parts of the F_2 adults reared at 10°C were calculated and are presented in table 26. They show the same trend as that of the F_2 generation at 27.5°C i.e. the correlations were better than those of

Table 26. Correlation coefficients for F_2 generation reared at 27.5°C.

			Antennal segment						
		Body length	3	4	5	6	Cornicle	Cauda	Tibia 3
Tibia 3		0.935	0.961	0.911	0.869	0.770	0.953	0.821	1
Cauda		0.829	0.795	0.689	0.540	0.534	0.873	1	
Cornicle		0.944	0.945	0.875	0.813	0.739	1		
Antennal segment	6	0.690	0.775	0.853	0.840	1			
	5	0.745	0.852	0.874	1				
	4	0.836	0.880	1					
	3	0.934	1						
Body length		1							

the F_2 generation. The poorest correlation was between the length of the 6th antennal segment and the body length ($r = 0.560$). To examine whether this trend persisted through the later generations at 27.5°C, the correlations between the same seven characters and the body length were determined and are presented in table 27. These coefficients were poorer than those of the F_1 for all the parts except the cauda. The poorest correlation was with the 6th antennal segment.

Although correlation coefficients show the level of association between body parts at a particular temperature regime, they fall short of indicating the trend of changes of the parts at different temperatures. To study this, the ratios of the body length to the various characters, and also the different parts to each other were

calculated and are illustrated in figs. 23 and 24 respectively. Data used for determination of the ratios were those of F_1 generation at 10, 20 and 27.5°C. Except for the body width and 5th antennal segment all ratios tended to decrease from 10 to 27.5°C, thus showing the increase of these parts relative to the body length. The body width exhibited the opposite of the above trend. The 5th antennal segment was relatively longer at 20°C than the other two temperatures (fig. 23).

Table 27. Correlation coefficients for

	F_2 at 10°C	F_5 at 27.5°C
	Body length	Body length
Tibia 3	0.709	0.731
Cauda	0.705	0.736
Cornicle	0.682	0.792
6	0.560	0.280
Antennal 5	0.714	0.417
segments 4	0.601	0.510
3	0.755	0.578

Fig. 24 shows the ratios between various parts at the 3 temperatures. Ratios of the 6th antennal segment to the 3rd segment, cornicle to cauda, tibia 3 to cornicle, tibia 3 to 4th antennal segment showed that they varied at the different temperatures. The ratios of body width to the 5th antennal segment, tibia 3 to the 3rd segment, cornicle to the 3rd segment were also variable but tended to a successive decrease from 10°C to 27.5°C, while the ratio of

Fig. 23. Ratios of body length of M. persicae to other body parts at three different temperatures.

Fig. 24. Ratios between various body parts of apterous virginoparae M. persicae at the three different temperatures.

Key

A_3 Third antennal segment

A_4 Fourth " "

A_5 Fifth " "

A_6 Sixth " "

Ca Cauda

Co Cornicle

T_3 Third tibia

W Body width

Fig.23.

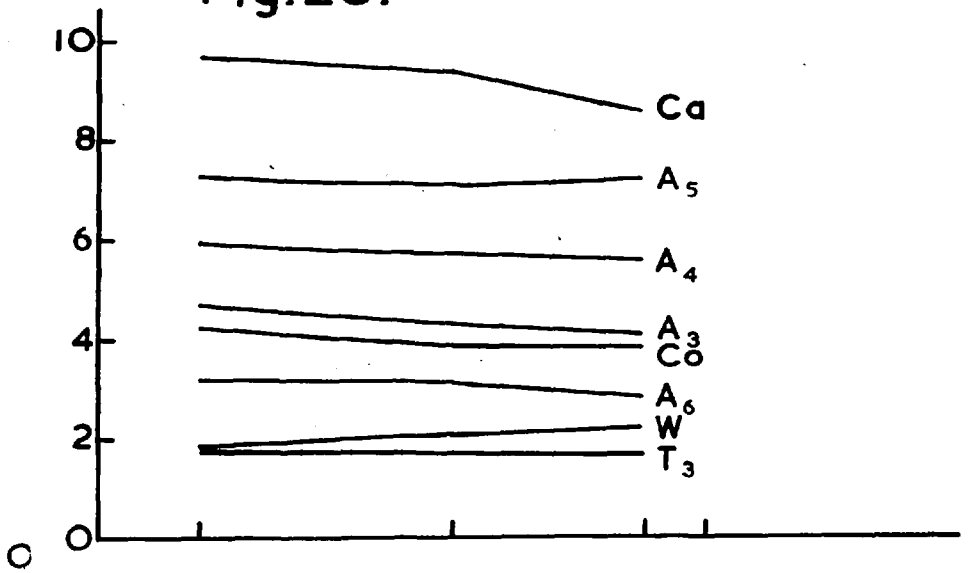
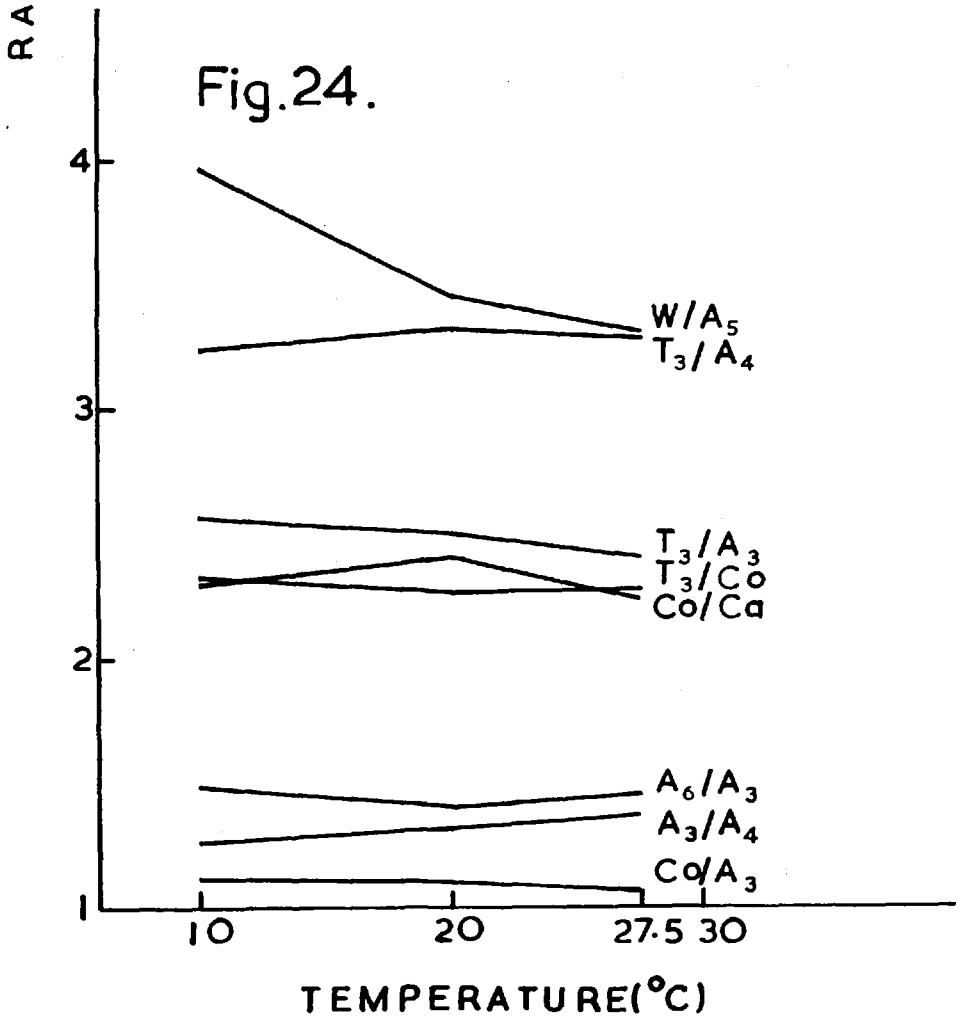

10
8
6
4
2
0
Ca
A_5
A_4
A_3
Co
A_6
W
T_3

Fig.24.


RATIO
4
3
2
1
W/A_5
T_3/A_4
T_3/A_3
T_3/Co
Co/Ca
A_6/A_3
A_3/A_4
Co/A_3
10
20
27·5
30
TEMPERATURE(°C)

the 3rd segment to the 4th segment showed the opposite trend.

The ratios of the body length to the various characters for all the different generations produced at 10°C, 20°C and 27.5°C are calculated and presented in table 28. The eleven generations are, arranged in the table according to the body lengths irrespective of the temperature treatment; the longest being in the F_2 at 10°C, and the shortest in the F_5 at 27.5°C. All the parts increased in size relative to the body length in the first four treatments, but decreased in the 5th treatment, except for the 5th antennal segment. No clear pattern is seen for the other treatments.

The effect of the different temperatures and treatments on tibia and cornicle, cornicle and 3rd antennal segment, 3rd segment and the 6th, body length and tibia 3 were further examined by regression analysis. Taking all the points, regression lines were calculated and presented in figs. 25 to 28. The changes in ratios between different parts noted above were also clear when the combined results of all the generations were analysed. In figs. 25 the ratios of tibia to cornicle in F_2 at 10°C and F_4/F_1 did not fit well the calculated line; they lay mostly above and below the line respectively. In fig. 26 ratios for F_2 at 10°C were mostly above the line. However, the most marked separation of ratios was noticed in figs. 28 where the body length ratio to tibia3 for F_1 at 10°C and F_2 at 10°C were remarkably high.

Table 28. Ratios of the body length to the other characters.

(Figures in parenthesis are body lengths in mm.)

	F_2 10°C	F_1 10°C	F_4/F_2	F_4/F_3	F 20°C	F_4/F_1	at 27.5°C				
							F_1	F_2	F_3	F_4	F_5
	(1.899)	(1.782)	(1.678)	(1.661)	(1.656)	(1.611)	(1.422)	(1.340)	(1.256)	(1.256)	(1.215)
Antennal segments 3	5.382	4.689	4.279	4.183	4.322	4.208	4.089	4.293	4.272	4.295	4.168
4	6.301	5.910	5.717	5.645	5.742	5.891	5.581	6.050	6.199	6.199	6.258
5	8.103	7.293	7.248	7.127	7.124	7.368	7.213	7.666	7.875	7.879	7.697
6	3.782	3.172	3.149	3.055	3.077	3.120	2.807	2.919	2.834	2.820	2.838
Cauda	10.526	9.682	9.239	8.912	9.380	8.778	8.616	8.433	8.296	8.481	7.985
Cornicle	4.589	4.201	3.884	3.768	3.903	3.774	3.859	3.967	3.962	3.911	3.775
Tibia 3	1.980	1.821	1.707	1.690	1.728	1.731	1.700	1.746	1.743	1.768	1.671

Fig. 25. Repression of the length of hind tibia on the length of cornicle of M. persicae adults reared for:-

one generation at 10°C (●)

two generations at 10°C (○)

continuously at 20°C (△)

one generation at 27.5°C (▲)

two " " " (□)

three " " " (■)

four " " " (◇)

five " " " (◆)

four generations at 27.5°C + one at 20°C (X)

" " " " + two " " (θ)

" " " " + three " (ϕ)

Fig.25.

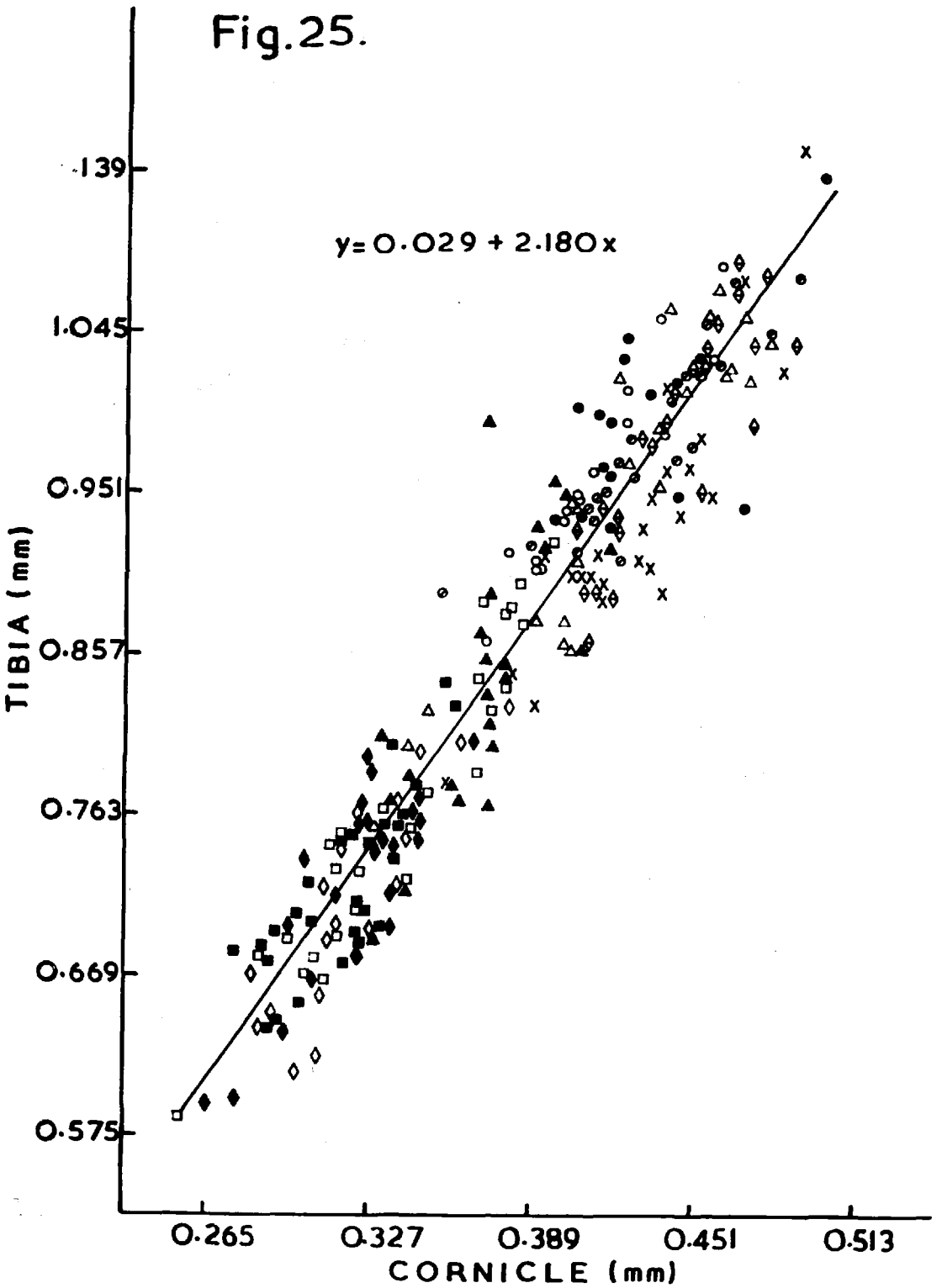

y= 0·029 + 2·180x
1·139
1·045
0·951
0·857
0·763
0·669
0·575
TIBIA (mm)
0·265
0·327
0·389
0·451
0·513
CORNICLE (mm)

Fig. 26. Regression of the length of cornicle on the length of the 3rd antennal segment of M. persicae adults reared for:

one generation at 10°C (●)

two generations at 10°C (○)

continuously at 20°C (△)

one generation at 27.5°C (▲)

two generations " " (□)

three " " " (■)

four " " " (◇)

five " " " (◆)

four generations at 27.5°C + one at 20°C (X)

" " " " + two " " (θ)

" " " " +three " " (⊕)

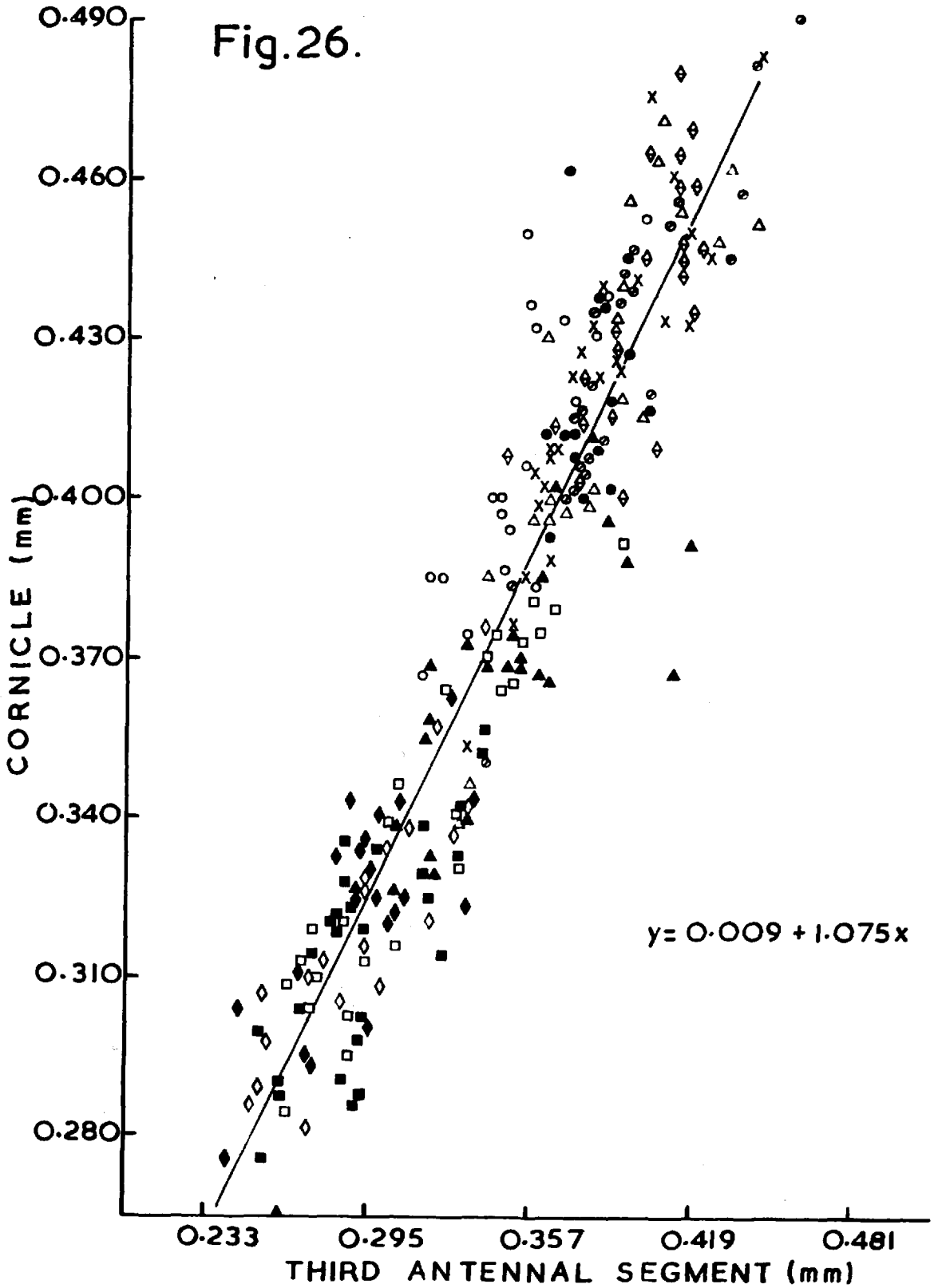


Fig.26.
0·490
0·460
0·430
0·400
0·370
0·340
0·310
0·280
CORNICLE (mm)
y= 0·009 + 1·075x
0·233
0·295
0·357
0·419
0·481
THIRD ANTENNAL SEGMENT (mm)

Fig. 27. Regression of the length of sixth antennal segment on the length of the 3rd antennal segment of M. persicae adults reared for:

one generation at 10°C (●)

two generations at 10°C (○)

continuously at 20°C (△)

one generation at 27.5°C (▲)

two generations " " (□)

three " " " (■)

four " " " (◊)

five " " " (◆)

four generations at 27.5°C + one at 20°C (X)

" " " " + two " " (θ)

" " " " +three " " (ϕ)

Fig. 27.

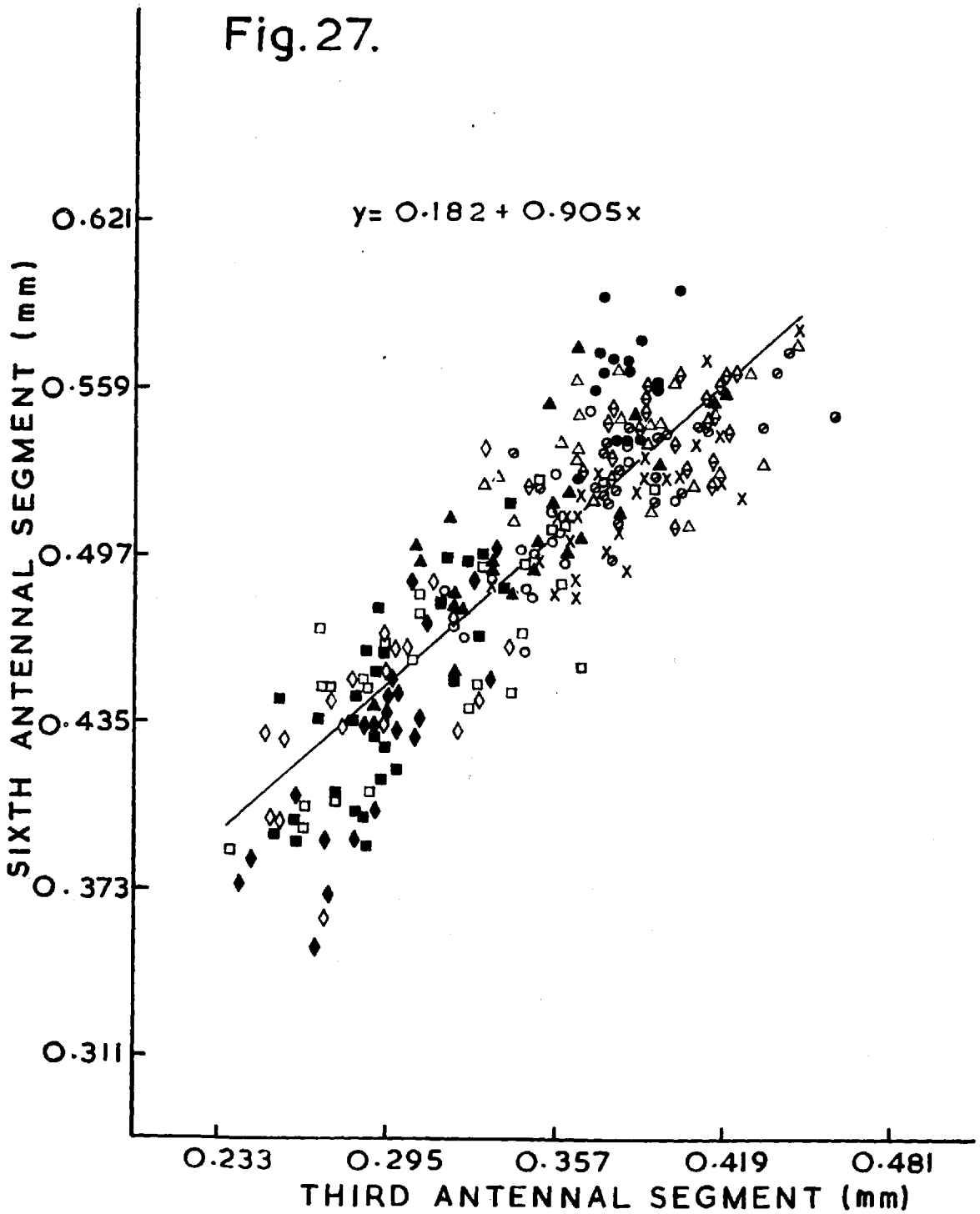

y= 0·182 + 0·905x
0·621
0·559
0·497
0·435
0·373
0·311
SIXTH ANTENNAL SEGMENT (mm)
0·233
0·295
0·357
0·419
0·481
THIRD ANTENNAL SEGMENT (mm)

Fig. 28. Regression of the body length on the length of hind tibia of M. persicae adults reared for:

one generation at 10°C (●)

two generations at 10°C (○)

continuously at 20°C (△)

one generation at 27.5°C (▲)

two generations " " (□)

three " " " (■)

four " " " (◇)

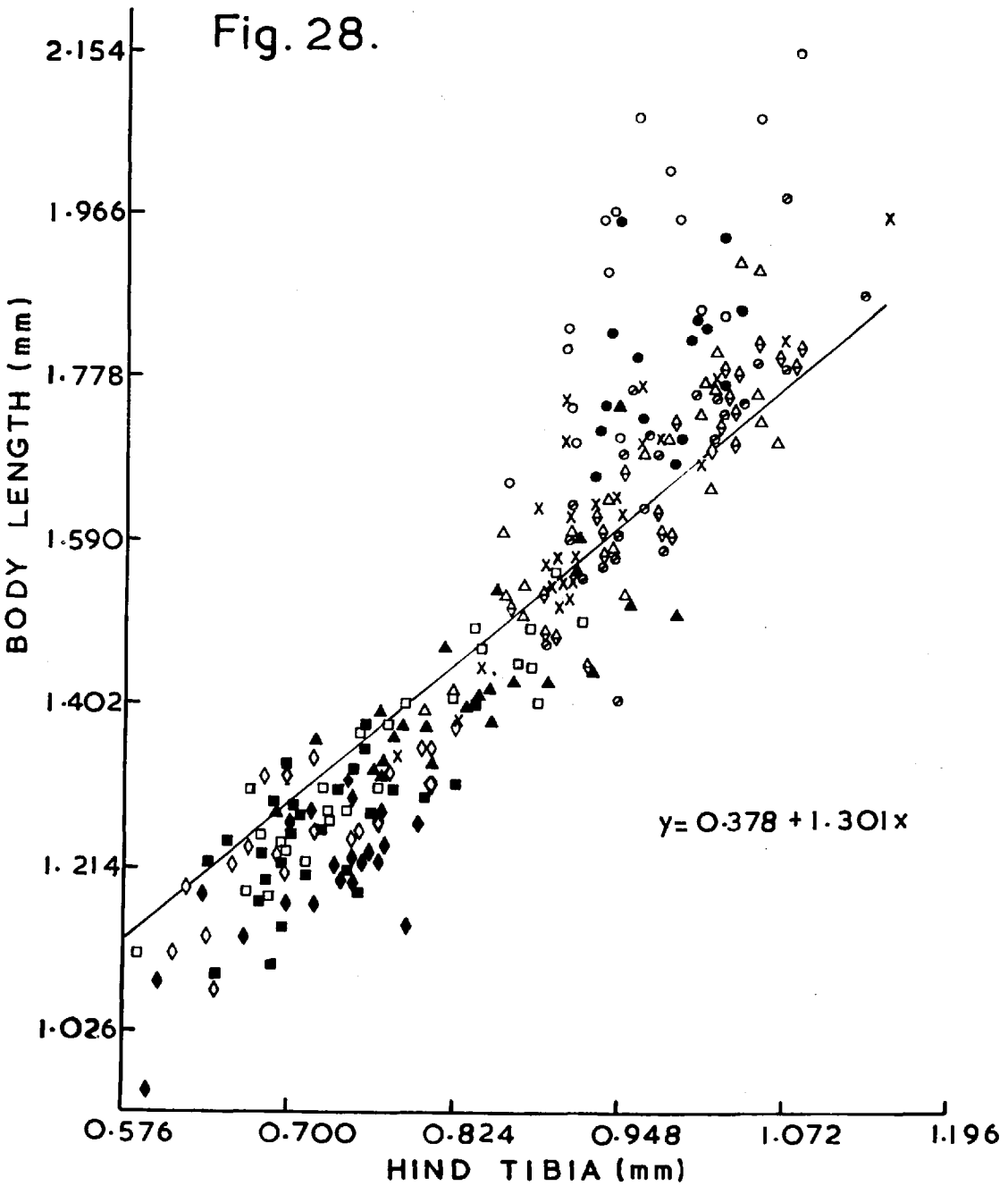
five " " " (◆)

four generations at 27.5°C + one at 20°C (X)

" " " " + two " " (⊖)

" " " " +three " " (⊕)

Fig. 28.


2·154
1·966
1·778
1·590
1·402
1·214
1·026
BODY LENGTH (mm)
y= 0·378 + 1·301x
0·576
0·700
0·824
0·948
1·072
1·196
HIND TIBIA (mm)

(4) Effect of size variation, caused by temperature, on development, fecundity, reproductive period and longevity.

The effect of temperature on the factors mentioned above is described in pages 85-107 . This part is concerned with the study of the body size changes, caused by the different temperature treatments, and its influence on developmental period, fecundity, reproductive period and longevity. The results examined in this section have already been discussed.

(a) Experiments at 27.5°C.

(i) Effect of size changes on developmental and pre-larviposition periods.

Five successive generations were reared at 27.5°C and the body lengths of the adult apterae in each generation determined as described on page 11 The larval development and the pre-reproduction periods were obtained for 9 successive generations at this temperature. The data for the 1st five generations were taken for the assessment of possible relationships between size and development. These and the body lengths of adults are presented in table 29.

Size and developmental period exhibited a steady decrease in the 1st 3 successive generations. The mean size of F_4 adults was equal to that of F_3, while the development time was insignificantly longer in the F_4 generation. In the F_5 they were both shorter than that of the F_4. Pre-reproductive period successively increased to the 3rd generation and then underwent successive decrease to the 5th generation.

Table 29. Mean values of body length (mm), development and pre-larviposition periods (hours).

Generation	Body length	Development period	Pre-reproductive period
F_1	1.422	135.5	14.4
F_2	1.340	133.9	15.0
F_3	1.256	131.6	19.5
F_4	1.256	138.4	16.2
F_5	1.215	137.8	14.1

Regressionsof development and pre-larviposition periods on body length were determined (fig. 29A and B). The two durations decreased with increase in size, $y = 144.52 - 7.00\ x$ and $y = 26.22 - 8.00\ x$ respectively.

(ii) Effect of size changes on fecundity, reproductive period and longevity. The mean body length of adult apterae for the 5 generations and also the mean fecundity, reproductive period and longevity of individuals kept at 27.5°C and those kept as adults at 20°C after each generation at 27.5°C are presented in table 30. At 27.5°C the 4 characters showed positive correlations with each other; the figures decreasing in the successive generations from the 1st to the 5th, except that the size of the F_4 was equal to that of the F_3. However, differences in reproductive period and longevity between F_4 and F_3 were negligible.

Fig. 29. The effect of the adult size on pre-reproduction (A) and developmental periods (B) of apterous virginoparae *M. persicae* reared at 27.5°C.

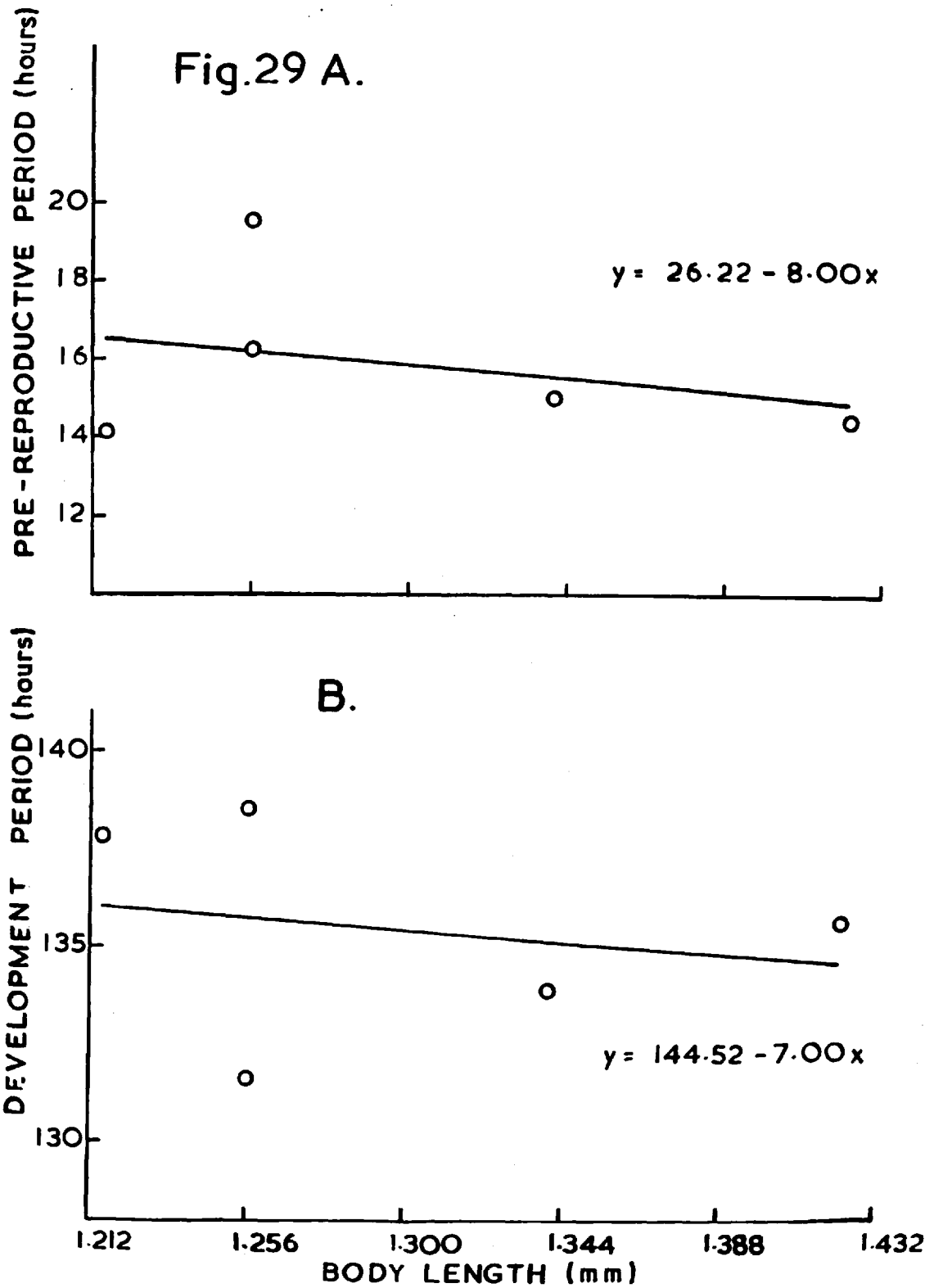


Fig.29 A.
PRE-REPRODUCTIVE PERIOD (hours)
20
18
16
14
12
y = 26·22 - 8·00x
B.
DEVELOPMENT PERIOD (hours)
140
135
130
y = 144·52 - 7·00x
1·212
1·256
1·300
1·344
1·388
1·432
BODY LENGTH (mm)

Table 30. Mean values of body length (mm), fecundity, reproductive period and longevity.

Generation	Body length (27.5°C)	Fecundity		Reproductive period (days)		Longevity (days)	
		27.5°C	20°C	27.5°C	20°C	27.5°C	20°C
F_1	1.422	33.5	14.0	8.9	6.6	12.2	9.3
F_2	1.340	20.8	19.8	7.4	10.2	9.5	13.6
F_3	1.256	8.8	19.5	3.6	9.2	5.5	12.0
F_4	1.256	5.9	22.0	3.4	13.2	5.3	15.8
F_5	1.215	1.8	16.8	1.2	10.5	3.4	13.0

Fecundity, reproductive period and longevity of adults of the same size returned to 20°C after each generation at 27.5°C showed almost the opposite trend. Fecundity steadily increased to F_4 and decreased in F_5. The reproductive period and longevity were shortest in the F_1 generation followed by increase and decrease in duration to the F_4 where they attained their maxima.

The regression of the 3 characters on size at the two treatments were calculated and presented in fig. 30 (A, B, &C). Fecundity and size decreased in the 5 generations reared at 27.5°C, $y = 171.02 + 142.66\ x$, but the progeny of adults tested at 20°C increased with decrease in size, $y = 42.65 - 18.67\ x$ (fig. 30C). The reproductive period and longevity showed a similar trend (fig. 30 A and B).

Fig. 30. The effect of the adult size on longevity (A), reproduction period (B) and fecundity (C) of apterous virginoparae *M. persicae* reared and kept at 27.5°C (○) and developed at 27.5°C and fecundity tested at 20°C after each generation (●)

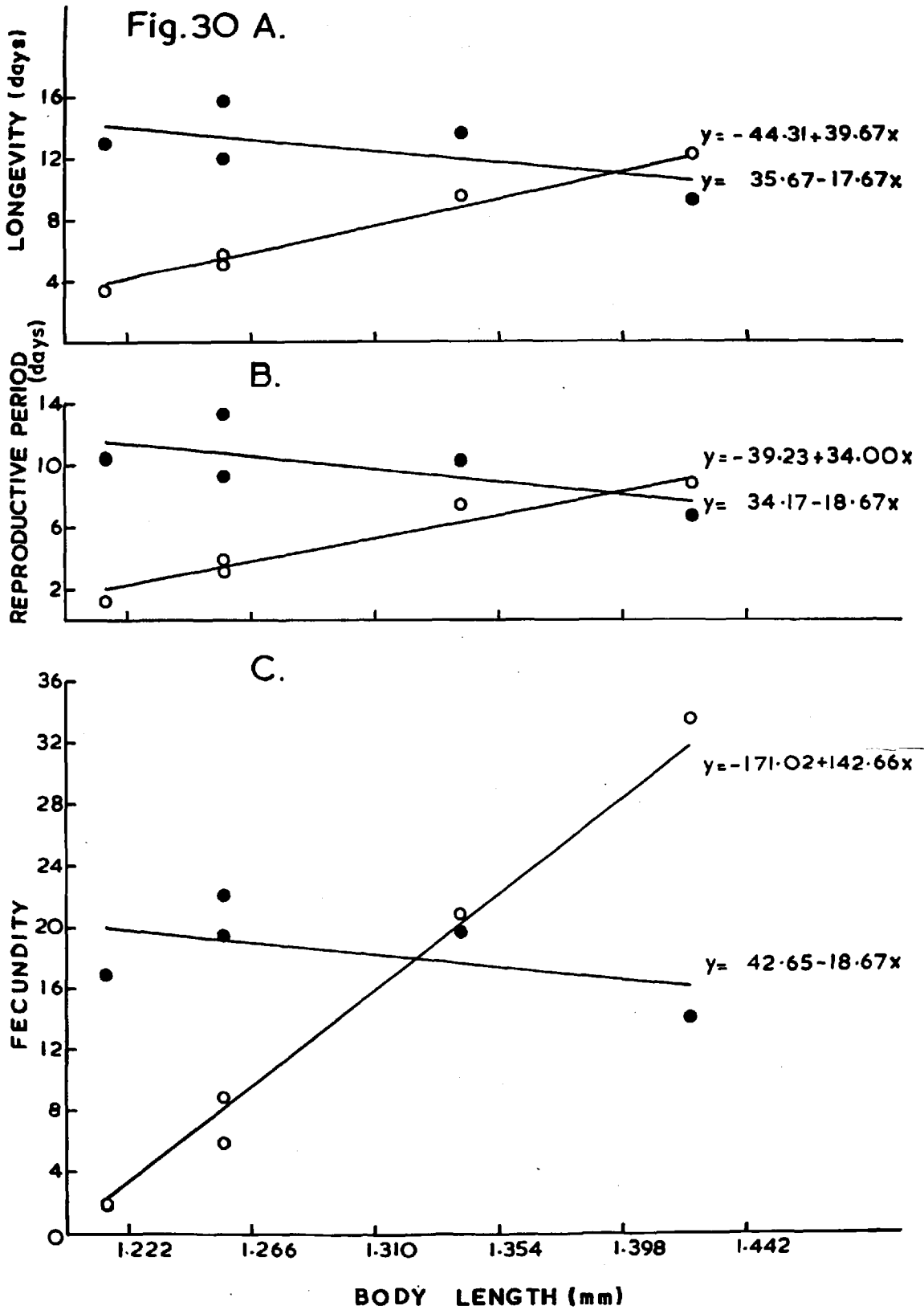


Fig.30 A.
LONGEVITY (days)
16
12
8
4
y = - 44·31 + 39·67x
y = 35·67 - 17·67x
REPRODUCTIVE PERIOD (days)
B.
14
10
6
2
y = - 39·23 + 34·00x
y = 34·17 - 18·67x
C.
FECUNDITY
36
32
28
24
20
16
12
8
4
0
y = - 171·02 + 142·66x
y = 42·65 - 18·67x
1·222
1·266
1·310
1·354
1·398
1·442
BODY LENGTH (mm)

Adults of the F_4 generation at 27.5°C were returned to 20°C and 3 generations were then reared. A summary of the adult size, fecundity, reproductive period and longevity is given in table 31. The size showed an insignificant increase in F_2 followed by a small decrease in F_3. The fecundity was almost equal for the 1st and 2nd generations, and insignificantly greater in the 3rd. The reproductive periods and longevities were not markedly different in the 3 generations.

Table 31. The mean size, fecundity, reproductive period and longevity after transfer from the 4th generation at 27.5°C to 20°C.

Generation	Body length (mm)	Fecundity	Reproductive period (days)	Longevity (days)
F_4/F_1	1.611	27.3	8.5	13.2
F_4/F_2	1.678	27.1	7.4	11.0
F_4/F_3	1.661	34.2	8.1	11.8

(b) Experiments at 10°C

Effect of size on fecundity, reproductive period and longevity.

Two generations were reared at 10°C. The adult size was determined at 10°C and fecundity at both 10 and 20°C after each generation. At 10°C the size of adults increased significantly in the second generation ($p < 0.01$), but fecundity, reproductive period and

longevity at 10°C decreased significantly in the 2nd generation at $p \leq 0.001$, $p < 0.001$ and $p < 0.05$ respectively. The same characters for adults kept at 20°C after developing as larvae at 10°C did not show any significant differences in the F_2 generation. However, fecundity of F_1 adults tested at 10°C was significantly less than those of F_1 and F_2 adults tested at 20°C, $p < 0.05$ and $p \leq 0.01$ respectively (table 31).

Table 32. The means of the four factors at the two temperatures.

Generation	Body length (mm)	Fecundity		Reproductive period (days)		Longevity (days)	
		10°C	20°C	10°C	20°C	10°C	20°C
F_1	1.782	19.4	33.5	14.6	8.1	18.7	9.5
F_2	1.960	5.6	34.7	5.8	9.2	13.5	11.5

E. DISCUSSION.

(1) Effect of high temperature on development.

Viviparous apterae M. persicae were reared for 9 generations at 27.5°C. The developmental periods (table 16) were all significantly shorter than at 20°C. Continuous rearing at 27.5°C did not alter the developmental period.

When adults, bred continuously for 4 and 9 generations at 27.5°C, were transferred to a suitable temperature (20°C), the developmental periods of the first genrations for both groups were slightly longer than that of individuals continuously kept at 20°C (tables 18 and 19). The durations in the subsequent generations at 20°C decreased steadily and this decrease was most noticeable with aphids reared for the longer period (9 generations) at 27.5°C. The lengths of F_4/F_3 and F_9/F_2 were significantly shorter than that of F_4/F_1 and F_9/F_1 at $p < 0.001$ respectively. The F_9/F_4 generation which was of the shortest duration (151.1 hours) was significantly shorter than F_4/F_4 (173.0 hours). These findings suggest that the sudden change to the favourable temperature results in a temporary relief from the high temperature stress, which later shows its effect on the succeeding generations. The fact that the individuals which were exposed longest to the high temperature completed larval development more quickly in the successive generations at 20°C than the ones reared for 4 generations at 27.5°C further supports this suggestion.

The significant increase in duration of F_9/F_5 (163.5 hours) compared to F_9/F_4 (151.1 hours) implies that the durations have possibly reached their minima and started to increase to approach that of the individuals continuously kept at 20°C (182.9 hours). The present experiments provide some information on the effect of continuous exposure to high temperature on the development period and its trend of changes after 4 and 9 generations when returned to a lower temperature (20°C). To give a more appropriate explanation of the effect of the temperature and to answer questions arising during this discussion, a study of the trend of changes at 20°C after each generation reared at 27.5°C is needed, also that of individuals kept continuously for a number of generations at 27.5°C when returned to a lower temperature is important.

(2) Effect of low temperature on some factors.

Aphids continuously reared and kept as adults at 10°C for 2 successive generations decreased in fecundity from 19.4 in the 1st generation to 5.6 in the 2nd. F_1 and F_2 generation adults reared as larvae at 10°C and then the fecundities examined at 20°C after each generation produced very similar numbers of progeny which were about double the number of that produced by F_1 generation kept at 10°C (table 22). This suggests that exposure to critically low temperatures for 2 generations has no long injurious effect on fecundity. These results agree with Murdie's (1965) who found that Acyrthosiphon pisum

kept as larvae at 10°C produced 20.5 and 67.6 nymphs/adult at 10 and 20°C respectively. Lees (1959) working on Megoura viciae reported that adults which ceased to reproduce at 8°C, when transferred to 20°C each produced about 4 nymphs. Barlow (1962) recorded the fecundity of Macrosiphum euphorbiae to be 34 at 5°C compared with 19 at 10°C for M. persicae. These results indicate that critically low temperature varies between species.

The reproductive periods were 14.6 and 5.8 days for F_1 and F_2 generations respectively at 10°C, and 8.1 and 9.2 days for F_1 and F_2 respectively at 20°C. In the F_1 generation the fecundity was about double at 20°C and the reproductive period was halved. In the second generation the fecundity at 20°C was about 7 times that at 10°C and the reproductive period prolonged to only about double of that at 10°C (table 22).

Aphids kept as larvae at 10°C and as adults at 20°C produced remarkably greater numbers of progeny than when kept continuously at 10°C but were less fecund than those reared and kept continuously at 20°C (table 22). However, reproduction, especially in the very early days was much faster than in those kept continuously at 20°C. These results indicate that embryo development proceeds further in larvae reared at 10°C than when reared at 20°C. The fact that the aphid produces more progeny in the first few days when transferred to a higher temperature (20°C), and has a comparatively shorter reproductive period creates a situation where the increase in number of the population

could be relatively great since these are important parameters for a high intrinsic rate of increase.

From the foregoing discussions it follows that alteration of comparatively cold and warm weather in nature might be more favourable for population growth of the aphid than continuation of either. This also reflects that results obtained from constant temperature experiments in the laboratory often cannot be applied directly to the field (Cloudsley-Thomson, 1953). This author stated that fluctuating temperatures have some special stimulating effects on insect development when compared with constant temperatures. The growth of host plant at constant temperature is also of importance in this connexion as plants might have a different food quality from those in the field, especially for aphids which are sensitive to physiological changes in plants (Kennedy, Lamb and Booth, 1958; Kennedy and Booth, 1959).

Literature reviewed on pages 73 - 78 signifies that the number of young produced by a species of aphid is dependent on its size; but experiments at 10°C show that although the size of F_2 generation adults was significantly greater ($p < 0.01$) than F_1 generation adults, their fecundity was significantly less at the same temperature ($p < 0.001$) (table 23). Also adults of F_1 and F_2 generations developed as larvae at 10°C, although of significantly greater size than adults continuously reared and kept at 20°C, when transferred to 20°C produced less than the smaller-sized adults reared continuously at 20°C (table 22 and 23). These results reveal

that the same temperature which suppresses the reproductive capacity of the aphid, promotes increase in size. Therefore interpreting aphid capacity for reproduction from its size, without knowledge of conditions at which it developed could be erroneous.

Results just described illustrate the effects of temperature changes on aphids reared as larvae at another temperature. This is not often similar to conditions prevailing in nature where there are diurnal variations in temperature which act on all different stages of development of the insect. In the laboratory this should be studied by experimenting in fluctuating temperature conditions whihh simulate the conditions in the field (e.g. Lamb, 1961; Messenger, 1964).

(3) High temperature as a stress factor.

The five successive generations bred at 27.5°C showed a steady decrease in fecundity and size in the subsequent generations (tables 22 and 23). This agrees with Murdie's (1965) results who found that A. pisum kept at 25°C produced decreasing numbers of progeny in the 3 generations. It follows that high temperature has injurious effects on the reproduction of the aphid, and that this effect is more severe the longer the exposure to the high temperature. The work at present is not adequate to explain the actual internal modifications which lead to these results. However, Uvarov (1931) attributed this to semi-starvation of the individuals while Lees (1959) suggested 'heat injury' to be the cause. It is inferred that the second hypothesis is more acceptable, because it was shown that when small-

sized starved adults resulting from over-crowding and small adults exposed to high temperature were transferred to a suitable temperature the previous over-crowded adults were quicker to recover and attain normal size, than the heat injured individuals which had not produced their normal number of progeny even in the 3rd generation (Murdie, 1965).

Long (1953) suggested that for insects to continue reproducing at a high temperature their size should not be less than a minimum. Any species cannot develop and produce unless it attains a size greater than this minimum. Size, however, is not the sole factor since individuals cease to reproduce at low temperatures while they are still much bigger than individuals reared at higher temperatures.

Aphids reared as larvae at 27.5°C and their fecundity tested at 20°C after each generation produced least progeny in the F_1 generation which then steadily increased in the following generations (table 22). However, their recovery in fecundity was not complete in any generation. Also aphids reared as larvae at 28°C and 29°C and then kept as adults at the same temperatures (28 and 29°C) and also at 20°C produced less progeny at 20°C; also at 28°C even the F_2 generation adults tested at 20°C produced less than adults kept continuously at 28°C and thus contrasts with the corresponding F_2 generation adults at 27.5°C which produced more. This could perhaps be because at 28-29°C the damage inflicted in the 1st generation is such that the adult is even more damaged when transferred to 20°C than when kept at 28°C to which some acclimatization may have

occurred. This however does not seem to be a satisfactory explanation of the differences in effects on larval development of 27.5°C and 28°C.

Aphids reared at 27.5°C and kept as adults at 20°C produced less progeny in the F_1 generation than the same adults at 27.5°C, while they produced more in the following generations. Murdie (1965) recorded similar results when he examined the fecundity at 28°C and 20°C of A. pisum adults reared as larvae at 28°C. His figures were 8.75 and 7.25 nymphs/adult respectively. These observations indicate that the sudden change of temperature at a comparatively short period is more suppressing than a transfer after a long period at the high temperature since aphids kept continuously at 27.5°C for 4 generations and then transferred to 20°C as adults produced more progeny than did the adults transferred at the 1 st generation (table 22).

Further evidence that the size effect on fecundity is altered by temperature is produced by the results with adults of the same size reared at 27.5°C but kept as adults at 27.5°C and 20°C (table 22 and fig. 15). The greater fecundity of adults kept at 20°C cannot be due to size difference of the adults.

When F_4 generation adults reared continuously at 27.5°C were returned to 20°C and reared for 3 successive generations, the F_3 generation adults produced almost equal numbers of progeny as F_1 generation adults reared and examined at 27.5°C (table 22), but were less fecund than those kept continuously at 20°C. Thus recovery

in fecundity was slow and was not normal by the 3rd generation at 20°C, while size recovery was comparatively quicker since by the 2nd generation the size was similar to that of adults continuously kept at 20°C (table 23). Murdie (1965) using A. pisum found that progeny of second generation adults reared continuously at 25°C almost recovered their normal size, when reared for 2 successive generations at 20°C, but fecundity was still low compared with that of adults continuously kept at 20°C. It can be concluded that the injurious effect of high temperature on fecundity is partly independent of size and that the effect on size is more easily reversed.

Experiments on the effect of temperature on the size of various parts of the body of viviparous apterae of M. persicae revealed that the interrelations between their sizes varied at the different temperatures. The body length was relatively greater than that of the other parts at low temperatures - (figs. 23 and 28). The lengths of the sixth antennal segment was perhaps the most unstable and most sensitive to temperature changes and exhibited poorest correlations with sizes of other parts in all treatments (tables 25, 25 and 27; fig. 27). There were also variations in different generations at the same temperature.

At 10°C, especially in the 1st generation, the correlations between sizes of different parts were poor (table 24). The correlation coefficient between cornicle length and that of the 6th antennal segment at this temperature was only 0.039. The correlations were

slightly better in the F_2 generation but still poorer than correlations at 27.5°C where correlation coefficients increased in the 2 successive generations (tables 25 and 26). However, the high correlations attained in the F_2 generation at 27.5°C did not persist and were poorer in the F_5 generation (table 27).

These variations occurred not only in individuals under temperature stress, but also in recovering individuals. Table 28 shows a range of the ratios in 3 successive recovering generations at 20°C. Also fig. 25 shows that the figures for ratios between lengths of cornicle and tibia 3 in the F_1 generation (X) occur below the calculated regression line. These results agree with the findings on page 16 on the relative sizes of 3rd and 4th antennal segments of the 3rd nymphal instar at different temperatures (table 6). Murdie (1965) working on A. pisum which is a bigger aphid than M. persicae found that the ratios between 2 body parts (lengths of tibia 3 and 3rd antennal segment) at the various temperature treatments could be divided into 2 groups and separate regression lines were calculated for each group.

It can be concluded that the variations in proportional sizes of the various body parts at different temperatures indicate that using ratios for taxonomic work to distinguish between the various instars could be erroneous.

SECTION IV. STUDIES ON SOME APHIDS INFESTING THE POTATO CROP.

A. INTRODUCTION.

Potato, Solanum tuberosum, is an important food crop planted in most parts of the world. It is attacked by a number of aphid species, the diversity and intensity of which varies from one country to another (Hille Ris Lambers, 1955; Galecka, 1959; Bishop, 1965 and Iotov, 1966) and also within different areas of the same country (Davies, 1935, 1939; Fisken, 1959a). The main aphid species attacking potatoes are the peach-potato aphid, Myzus persicae (Sulzer), the potato aphid, Macrosiphum euphorbiae (Thomas), the buck thorn-potato aphid, Aphis nasturtii (Kalt), the glass house-potato aphid, Aulacorthum solani (Kalt) and a few others which are relatively rare. These inflict direct damage to the plant by ingesting nutrients and excreting honeydew on the surfaces of leaves (Kennedy and Stroyan, 1959; Banks, 1965). But the major damage caused is indirect, and is the result of some of these acting as vectors to transmit virus diseases (Davies, 1934; Bawden, 1943; Bishop, 1959). It is due to the latter cause that the potato yield suffers heavy losses when conditions for the spread of the disease are favourable (Johnson, 1964) and this has warranted much work on the ecology of these aphids and the factors affecting their growth in the crop.

Aphid populations on many plants are well below the potential number which the food could support (Sanders and Knight, 1968) and their level of infestation on potato has shown considerable variations.

Factors governing these changes have been a cause of controversy among different investigators.

The aim of this work was to study the intensity of the aphid population for a number of years on a potato plot in connexion with the main biotic and abiotic factors which are thought to be responsible for the fluctuations in their populations. A potato plot, situated in Silwood Park, was surveyed in the years 1967 and 1968 and the different aphid species encountered on the plants were counted. Climatic factors (temperature and rainfall) and the number of parasitized aphids, predators and infected aphids were recorded.

The density and time of the arrival of alatae on the potato crop is known to be an important factor governing the level of infestation by aphids (Fisken, 1959a; Daiber, 1964). Climatic factors affecting their immigration and their movement within the crop have caused controversy. The present work included a study of the aerial density of the aphid and also movement of the alatae within the crop using yellow water traps (Moericke, 1951).

B. MATERIALS AND METHODS.

(1) Aphid counts.

Two plots of potato, variety Majestic, were surveyed in the years 1967 and 1968. The planting dates were the same in the two years (25th April). The plot surveyed in 1967 was 30 m. long and 20 rows (90 cm apart) wide. The plants were spaced at 45 cm on the ridges and were about 6" tall at the beginning of the survey (14th June). The plot surveyed in 1968 was 50 m. long and 40 rows

wide. Sampling started (31ST May) a few days after emergence of the plants which had become infested earlier.

The plots were subdivided into 25 units and samples were taken from these units. Surveys were done twice a week in 1967 and once a week in 1968 except when the field was wet in which case the interval was prolonged. On the sampling days 25 stems, each from one unit, were cut very carefully and placed in cellophane bags and taken to the laboratory. Leaves were removed and the different aphid species on them were recorded and identified using mainly the key by Edwards and Heath (1964). The total numbers of each species other than M. persicae were recorded according to species as they were removed from the leaves. All stages and forms of M. persicae were transferred to a petri-dish containing 30% alcohol and the different stages were separated under a low power binocular microscope using Sylvester's (1954) method. The alatae, apterae, the four apterous nymphal stages and the 4th alate nymphal stage were recorded separately.

(2) Natural enemies.

Natural enemies found with the aphids were also identified. Three species of coccinellid predators were recorded. In 1967 surveys the adults and larvae were bulked, but in 1968 adults were identified to species level and recorded separately and the eggs, larvae and the pupae of the three species were added together. Syrphid eggs and larvae were collected and identified. Anthocorid adults and nymphs; spider mites and Chrysopid larvae were also

recorded. The numbers of aphid mummies without exit holes were also counted and were kept in sample tubes and the emerging parasite adults from each aphid species were identified. Fungus infected aphids were also counted and identified.

(3) Plant growth.

On each sampling day 5 rows were chosen at random and the number of stems in each plant counted along 10 m. length on the row. The mean number of the stems/plant and also number of aphids and natural enemies/100 plants were calculated.

(4) Trap catches.

To examine the early colonization of the plants by alatae of M. persicae and their movement within the potato crop 12 water traps were laid out within the plot. Plastic containers of 10 cm. diameter and 4 cm deep were painted green on the outside and on the top 1 cm of the inside; the bottom and the inside walls were painted yellow. A portion of about 1 inch x 1 cm was cut off from the edge of each container, and a piece of muslin stuck to this gap from the outside to stop overflowing when it rained. The containers were supported on stands placed in the furrows and the heights were changed with the growth of the plants to keep them level with the young leaves i.e. the traps were not covered with the vegetative growth. The containers were filled with a liquid made up from 1 gallon of water mixed with 20 cc of stergene-formalin and were topped up about twice a week or cleaned and refilled when necessary.

Collections of all alate aphids were made on alternate days in 1967 and twice a week in 1968. The aphids were examined under a binocular microscope and alate M. persicae were counted separately and all other species counted collectively.

Data from a "Rothamsted survey suction trap", sampling 100,000ft^3/ hour at a height of 40' through a 10" diameter pipe and situated about 30 m. from the plot was used to examine aerial distribution of the alatae. The results obtained from the potato samplings were compared with those of the traps.

(5) Meteorological data.

Temperature was continuously recorded by a thermograph with the measuring probe placed in the middle of a plant with lush growth. Rainfall, relative humidity and wind speed were obtained from the Meteorological site at Silwood Park.

(6) Potential rate of increase.

The theoretical rate of increase was calculated from the actual numbers on the plants. Hughes (1963) in this connexion classified population increase of Brevicoryne brassicae on kale as unimpeded, potential and observed increase. The difference between the first 2 terms is the effect of pre-reproductive mortality on the reproductive rate, while that between the 2nd and 3rd is the effect of all biotic and abiotic mortality factors.

For the present work the potential rate of increase was calculated from the observed numbers. In 1967 samplings number 1, 5, 10 and 14 were used to calculate the potential number of aphids developing during the following 2 - 7 weeks (fig. 33). In 1968 the potential number at each sampling was calculated from the actual numbers in the previous sampling.

Results of experiments conducted in controlled environment rooms (page 37) were used to calculate the potential rate of increase at different temperatures. The increase in number in the early stages of the population growth depends basically on the number of reproducing apterae and on immigrant alatae and their reproductive rate. Experiments on page 37 did not include a study on the fecundity and reproductive period of alatae, but previous work on aphids indicated that the apterae were more fecund than them (Lal, 1950; Hafez, 1961; Sanders and Knight, 1968). Lal recorded 25 and 15 progeny per aphid for apterae and alatae M. persicae respectively at 18°C and also 30 and 21 respectively at 23°C; this showed that there was a difference of about 10 nymphs per parent between the 2 forms. When calculating the potential population increase from the data, the following considerations were borne in mind.

- Early instars, which showed no wing buds, were assumed to develop into adult apterae.

- Alatae arising from nymphs produced on the crop were considered as emigrating adults leaving the crop without reproducing.

- All the stages counted in the different samplings were assumed to be middle aged in the particular instars in which they were found,

whether larval or adult.

The method adopted in the present work for calculating the potential numbers for the various counts was a long one. The intrinsic rate of increase, which is quicker, was not used because this parameter could only be used in conditions where the population has attained a stable age-distribution (Birch, 1948). Since in the field both selective and non-selective mortalities operate together (Hughes, 1963), the possibility of a population attaining a continuous stage age-distribution is remote. No attempts have been made previously with aphids to find the proportions in which the different stages occur when there is a stable age-distribution. An attempt is however made here to find, from the present observations, which ratios of the different stages possibly gave a stable age-distribution. Each observation with its instar-distribution was taken and the potential number was calculated by multiplying the number of adults counted on the plants as well as larvae attaining maturity by the number of nymphs they produced between sampling periods. The figure thus obtained was the unimpeded rate of increase from which the number due to pre-reproductive-mortality was subtracted. The same sampling data was used to calculate the potential number using the intrinsic rate of increase in the formula $Nt = Noe^{rt}$ (Barlow, 1962), where No = number of insects at time zero, Nt = number of insects at time t and r = intrinsic rate of increase. The instar-distribution which gave the same result with both these methods was considered to be close to the stable instar-distribution for M. persicae.

C. RESULTS.

(1) 1967.

(a) Aphid species on potatoes.

Alatae immigrants started to colonize potato plants late in the 2nd week of June. Species recorded, in order of abundance, were M. euphorbiae, A. nasturtii, M. persicae, R. latysiphon and A. solani The latter two species were detected as alatae only in the early samplings(table 33). Alate M. persicae were comparatively numerous in the 1st survey but subsequent population growth was slow. The populations of M. persicae oscillated and reached a peak about mid-July (table 33and fig. 31). The decline afterwards was sharp and the population remained low until September when it exhibited a slight resurgence followed by extinction.

The instar-distribution of M. persicae (table 33 and fig.32B) showed that the different instars and the 2 adult forms were present in the 1st two surveys, but for the rest of the surveys the 1st and the 4th instar apterae (4a) were least prevalent. Fig.32A shows the % of the different instars in the total population.

M. euphorbiae started with a few alatae compared with M. persicae and their build-up was rapid and attained its 1st peak by the end of June, afterwards declining to extinction by mid-August. However, numbers increased again to a 2nd greater peak in early September but the population again declined (table 33 and fig. 31).

Table 33. Aphid population on 100 potato plants at Silwood Park, 1967.

No.	Date	Instar and form of M.persicae							M.euphorbiae	A.nasturtii	A.solani	R.latysiphon
		1	2	3	4a	Aptera	Alate	Total				
1	16.6	35	30	35	5	10	60	175	205(10)*	150(35)	-(5)	-(5)
2	19.6	42	42	28	7	14	21	154	1554(28)	392(315)	-	-
3	23.6					8		8	768(48)	224(192)	-(8)	-
4	27.6		17	17			9	43	1921(68)	501(60)	-	-(17)
5	1.7					23		23	1357(46)	1265(58)	-	-
6	6.7		14	14		14		42	1274(28)	616(14)	-	-
7	10.7	16	50	50		16		132	1188	1600(132)	-	-
8	14.7	462	759	313	66	50	99	1749	314(17)	610(17)	-	-
9	19.7	79	557	265	212			1113	636	1908(53)	-	-
10	24.7				27			27	53	371(27)	-	-
11	29.7			30				30	30	-	-	-
12	3.8		31		31	31		93	62	-	-	-
13	7.8			62				62	124	155	-	-
14	15.8				34			34	-	34	-	-
15	25.8			36				36	1242	213	-	-
16	10.9	36	106					142	2627	71	-	-
17	25.9							0	750	-(38)	-	-

* No. of alatae.

Fig. 31. Populations of potato aphids on a potato crop at Silwood Park, 1967 with daily maximum, mean, minimum temperature and rainfall.

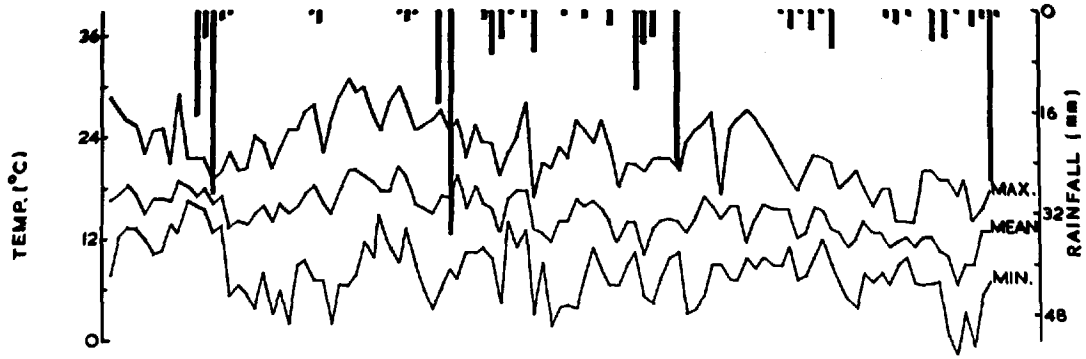

TEMP.(°C)
36
24
12
0
MAX.
MEAN
MIN.
16
32
48
RAINFALL (mm)

Fig. 31. 1967

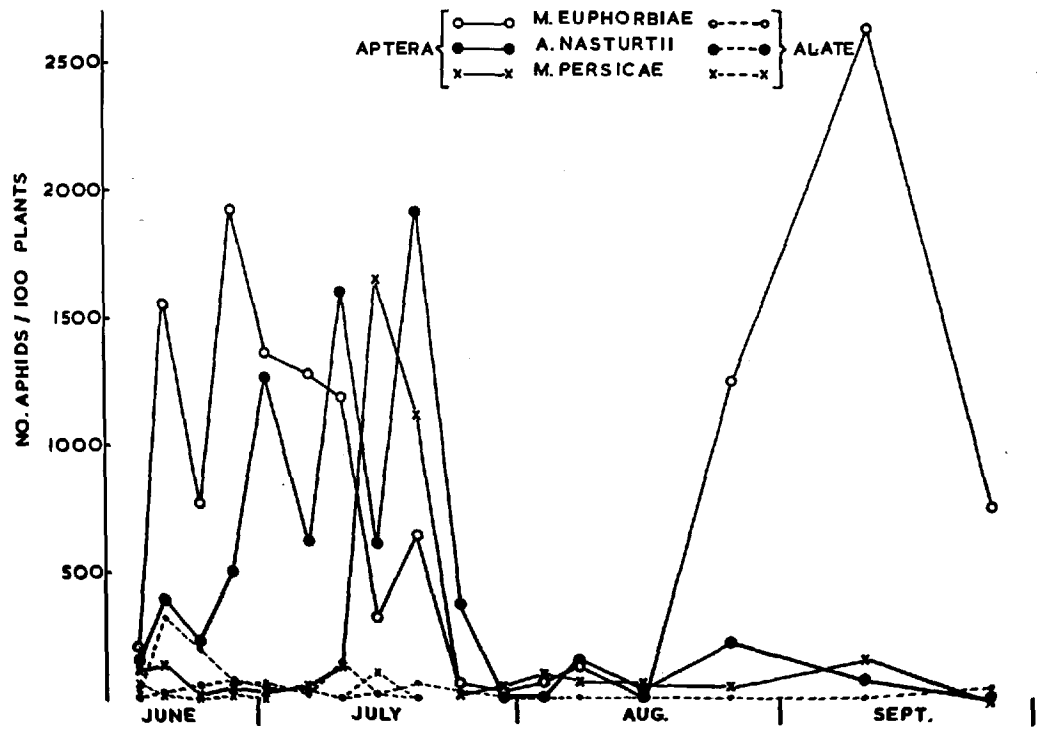

APTERA
M. EUPHORBIAE
A. NASTURTII
M. PERSICAE
ALATE
NO. APHIDS / 100 PLANTS
2500
2000
1500
1000
500
JUNE
JULY
AUG.
SEPT.

Fig. 32. Proportions of the various nymphal instars in the different samplings of 1967.

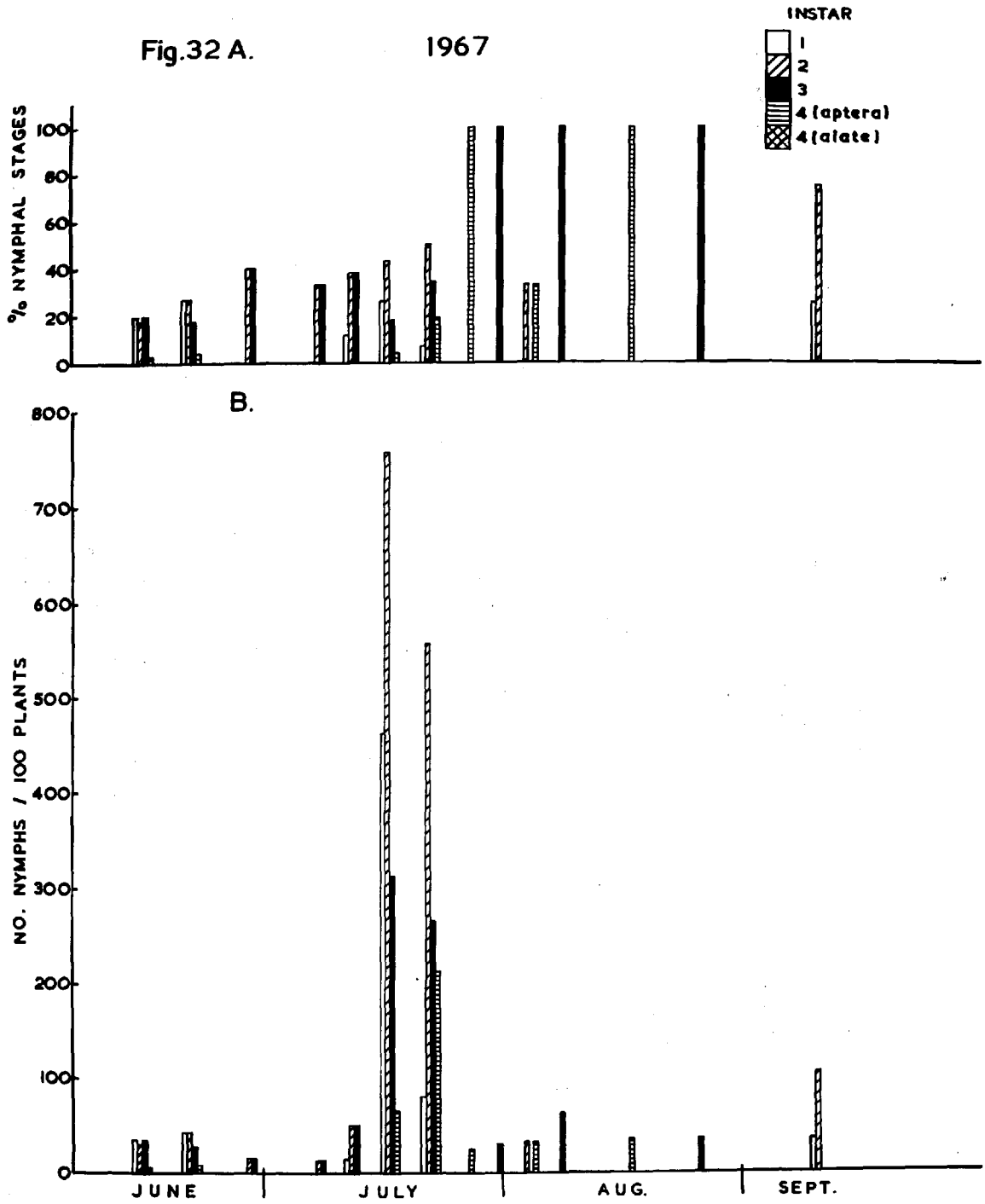


Fig.32 A.
1967
INSTAR
1
2
3
4 (aptera)
4 (alate)
% NYMPHAL STAGES
0
20
40
60
80
100
B.
NO. NYMPHS / 100 PLANTS
0
100
200
300
400
500
600
700
800
JUNE
JULY
AUG.
SEPT.

A. nasturtii followed almost a similar trend as M. euphorbiae in undergoing a steady rapid increase though the high population persisted longer until in July it virtually disappeared; later a small resurgence ensued and again the population died out by the end of September.

The three species showed different pattern of distribution on the plants. M. persicae was mainly found on the top young leaves and the bottom senescent leaves. M. euphorbiae preferred the upper half of the plant and was found exclusively on the inflorescence when the plant flowered. A. nasturtii colonized the lower half of the plant mostly the lower old leaves. M. persicae and A. nasturtii are slow moving aphids compared with M. euphorbiae.

The potential number of M. persicae was calculated from the field counts and is presented in table 34 and fig. 33. The potential numbers steadily increased with time, but the observed was inconsistent, showing rise and fall and was quite negligible compared with the theoretical numbers except about mid-July when M. persicae was most common.

Table 34. Potential and observed populations of M. persicae on potatoes. 1967.

Sampling number							
1 (16.6)		5 (1.7)		10 (24.7)		14 (15.8)	
Potential	observed	Potential	observed	Potential	observed	Potential	observed
	175		23				
1085	154	518	42	265	27		34
2928	8	2277	132	821	30	1072	36
13591	43	12145	1749	2496	93	27761	42
44838	23	161093	1113	28994	62	617078	0
		492980	27		34		

Fig. 33. Calculated potential and observed rates of increase of *M. persicae* on potatoes.

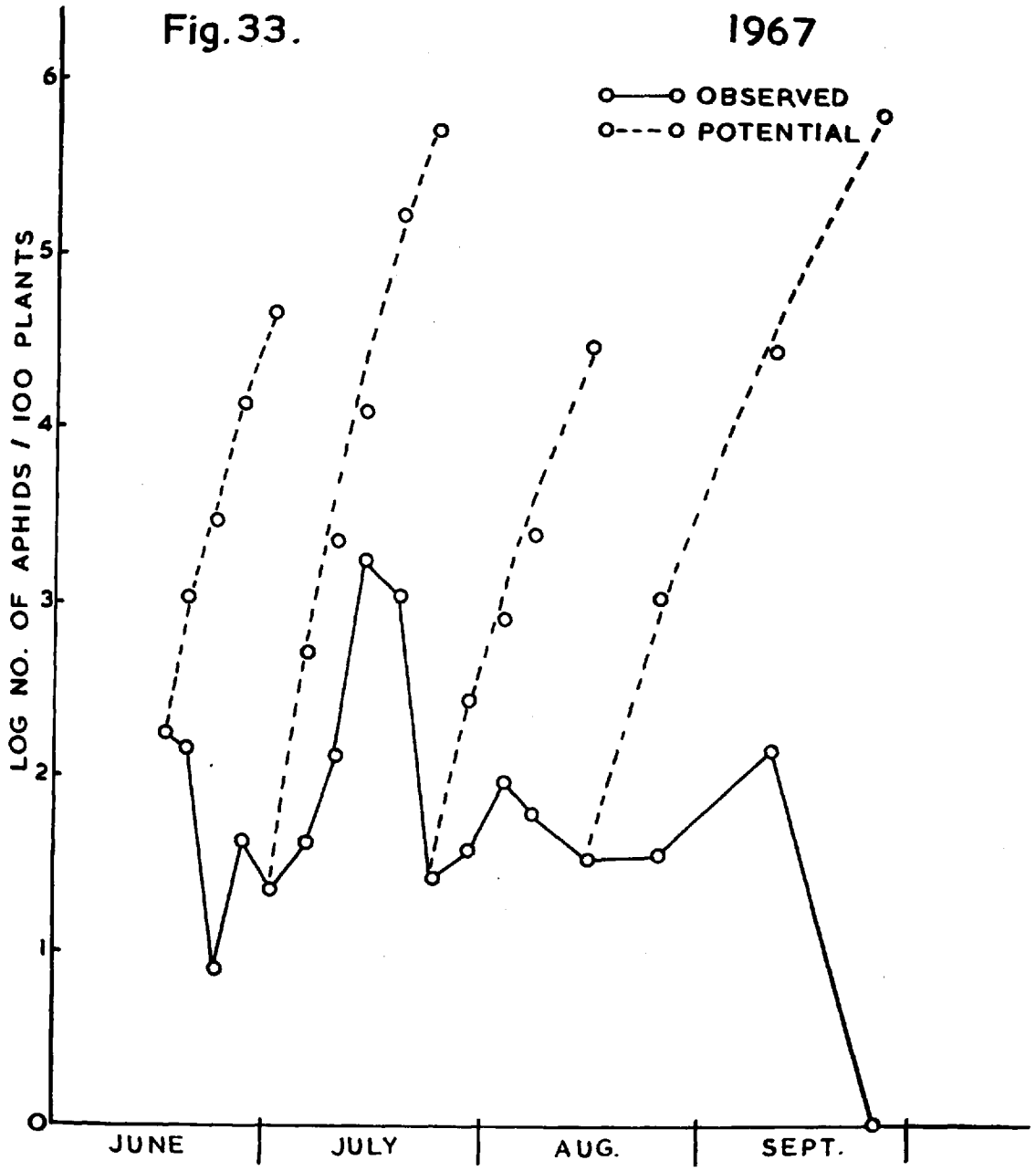


Fig. 33.
1967
OBSERVED
POTENTIAL
LOG NO. OF APHIDS / 100 PLANTS
0
1
2
3
4
5
6
JUNE
JULY
AUG.
SEPT.

(b) Natural enemies of potato aphids.

A summary of the natural enemies associated with potato aphids is presented in table35 . Coccinellids, syrphids and parasites appeared almost together, early in the season. The coccinellid species recorded, in order of abundance, were Coccinella septempunctata, Adalia bipunctata and Propylaea quattuordecimpunctata. They first appeared on weeds infested with aphids outside the plot and moved from there to the potato plot. They increased in number within the crop and disappeared late in July. A number of syrphid species including Syrphus balteatus, S. corollae, Platycheirus peltatus, S. ribesii, S. eligans and Melanostoma spp. were recorded; the 1st three were the dominant ones. Their numbers increased to a peak about the 1st week of July and then declined to the end of July when no records of them were made until mid-August after which they persisted to the end of the season.

A number of parasite adults emerging from mummies collected during the surveys were identified by the staff of the British Museum. These included Aphidius matricarie, A. nigripes, Diaeretiella rapae, Aphelinus basalis and Lygocerus rufiventris. The latter species is possibly a hyperparasite. The former 3 species mainly attacked M. persicae and A. nasturtii to a lesser extent, while the latter two species emerged from M. euphorbiae mummies. The % M. euphorbiae attacked by parasites were negligible compared with the number of parasitised M. persicae. The number of parasitized aphids increased with the progress of the season and attained their highest number early in August and disappeared shortly before the end of the season.

Table 35. The number of Myzus persicae Sulz and some of its natural enemies on 100 potato plants at Silwood Park, 1967.

No.	Date	M. persicae	Coccinellids	Syrphids	Chrysopids	Anthocorids	Mites	Mummies	Infected
1	16.6	175	0	0	0	0	0	0	0
2	19.6	154	42	28	0	0	0	14	0
3	23.6	8	16	64	0	0	0	40	0
4	27.6	43	17	43	0	0	0	17	36
5	1.7	23	46	127	0	0	0	81	81
6	6.7	42	14	126	0	0	0	154	84
7	10.7	132	33	182	0	0	0	165	50
8	14.7	1749	17	10	0	0	0	182	116
9	19.7	1113	26	53	0	52	0	371	0
10	24.7	27	0	27	0	0	0	186	0
11	29.7	30	0	0	0	0	30	207	0
12	3.8	93	0	0	0	31	0	465	0
13	7.8	62	0	0	62	0	62	31	0
14	15.8	34	0	34	34	34	0	268	0
15	25.8	36	0	177	107	36	36	0	0
16	10.9	142	0	71	36	142	0	0	0
17	25.9	0	0	38	0	150	38	0	0

Entomophagous fungi, possibly Entomophthora sp. (MacLeod, 1955; Ramaseshiah, 1967) attacked aphids in the field. A very high % of the infected aphids were M. euphorbiae and only a negligible number of M. persicae and A. nasturtii were attacked. A fungal disease, which was found growing on the legs of M. persicae culture in the controlled environment 15°C room, was not detected in the field on any of the aphid species. During samplings infected aphids were first observed from late June to mid-July, after which they disappeared.

Other apparently less important natural enemies were chrysopids, possibly Chrysopa carnea (Dunn, 1949), anthocorids and mites. The numbers presented in table 35 are the larvae of chrysopids, nymphs and adult stages of anthocorids and mites. The three predators appeared late in the season and persisted in small numbers to the end of the season.

(c) Trap catches.

Alate M. persicae and the total of all alate aphids caught in the water traps are presented in table 36. The greatest number of M. persicae was caught in mid-July, at a time when the catches of other aphids in the water traps and counts on the potato crop reached their peak. From mid-July the numbers declined and they disappeared later in the month.

Table 36. Trap catches of alate M. persicae and other species, 1967 and 1968.

Date	Suction trap		Water traps			
	1968		1967		1968	
	M. persicae	Total all species	M. persicae	Total all species	M. persicae	Total
2.6	19	147				
4.6					40	143
7.6	22	206			1	67
10.6					3	51
13.6					16	72
16.6	16	452	1	996	12	118
20.6			-	194	9	60
23.6	10	264	4	402		
24.6			4	407	2	35
27.6			-	160	4	28
30.6	2	286	-	235	1	26
3.7			-	88	4	28
6.7					7	84
7.7	43	2810	2	163		
9.7			15	477	2	31
12.7					1	58
14.7	19	4343	34	1024		
15.7					-	25
18.7			5	252	-	17
20.7	17	2636	4	113		
23.7			2	199	-	31
25.7			-	86	-	15
28.7	8	1028	-	47	-	9
31.7			-	40	-	12
4.8	3	776	-	33	1	18
7.8			-	15	-	4
11.8	-	424	-	5	-	14
13.8			-	3		
15.8			-	-	1	1
18.8	-	40	-	2		

(2) 1968.

(a) Aphid species on potatoes.

Alate aphids were observed on the potato plants directly after emergence in the 2nd half of May. Species recorded, in order of abundance, were M. euphorbiae, M. persicae and Aulacorthum solani (table 37 and fig. 34). M. euphorbiae increased rapidly on the crop and reached its peak late in June and then crashed to extinction by the end of July. However, late in the season it showed a slight resurgence as in 1967. M. persicae underwent a steady increase and attained its highest numbers by the end of June, afterwards decreasing slowly through the season, A. solani appeared slightly later than the other two, multiplied to only a small number in the middle of the season and was not observed in the later part of the season.

The instar distribution of M. persicae (table 37 and fig. 35) showed that in almost all the samplings the 1st instar outnumbered each of the other instars; its highest number coincided with the peak of the total population. It was also noticeable that in the middle 3 samplings when the population was highest(numbers 4, 5 and 6) the percentages of each of the 4 nymphal instars remained similar (fig. 35A). Using the two methods already described it was found that sampling No. 2 produced almost the same number.

The potential and observed numbers (table 38 and fig. 36) illustrated that the differences between them were small at the beginning of the season when the aphid population was steadily increasing,

but the gap started to widen just before the peak population on the plants when the population increase was slow and also when the population was declining in early July.

Table 37 . Aphid populations on 100 potato plants at Silwood Park, 1968.

No.	Date	Instar and form of M. persicae									
		1	2	3	4a	4w	Aptera	Alate	Total	M. euphorbiae	A. solani
1	31.5	124	64	36	8	0	0	76	308	520(68)*	0
2	7.6	360	380	210	70	0	20	170	1210	1170(50)	0
3	13.6	983	378	239	339	0	333	83	2355	5678(50)	72
4	20.6	3683	2725	1608	1067	25	1200	158	10466	35608(358)	391
5	30.6	5400	4920	2840	1360	1000	1620	160	17300	26100(1300)	240
6	15.7	2325	1825	1200	1000	225	825	100	7500	525(25)	25
7	29.7	180	300	150	120	0	30	0	780	0	60
8	5.8	90	90	150	60	0	90	0	480	60	0
9	13.8	120	30	90	30	0	120	0	390	30	0

* No. of alatae

Fig. 34. Populations of potato aphids on a potato crop at Silwood Park, 1968 with maximum, mean, minimum temperature and rainfall.

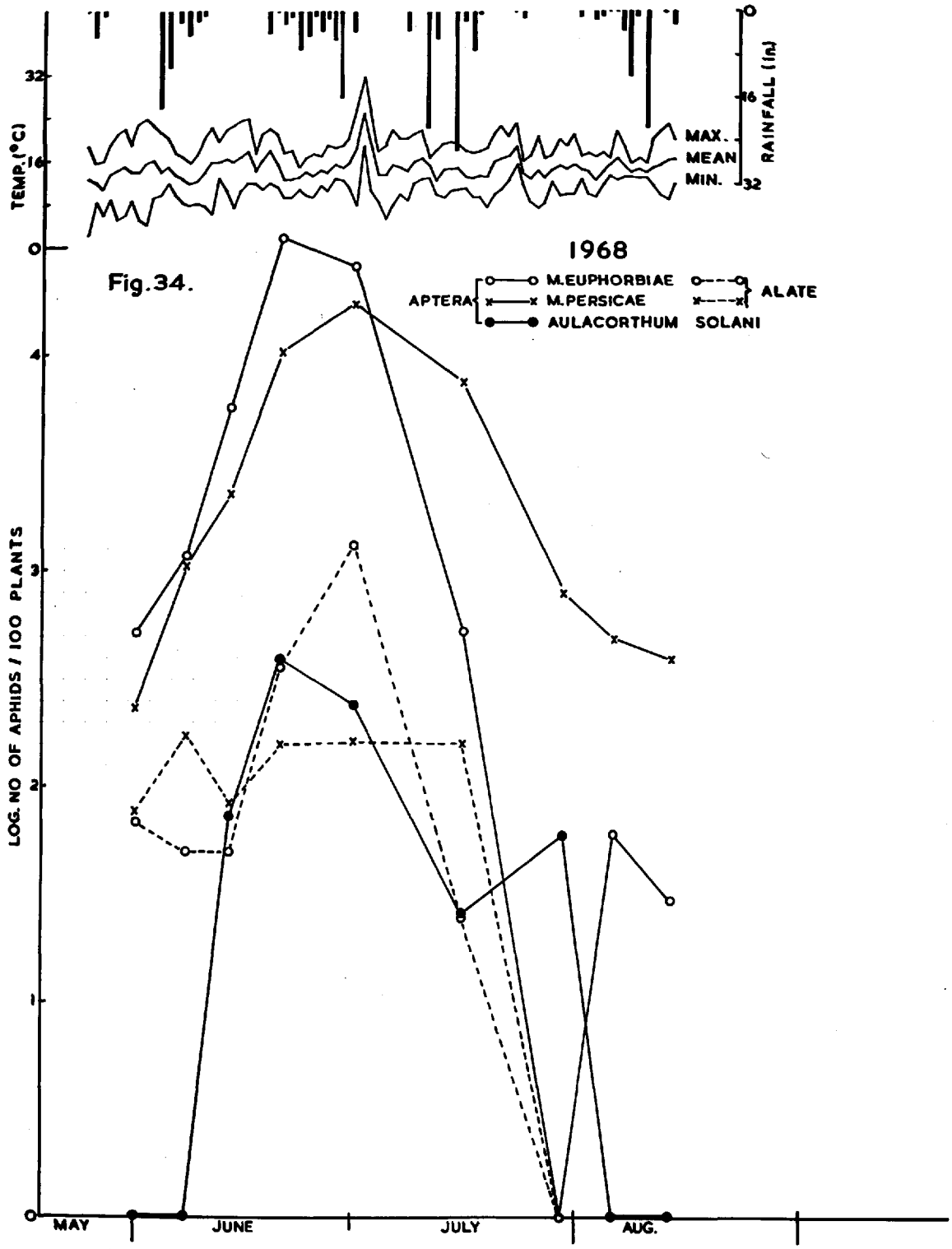

TEMP.(°C)
32
16
0
RAINFALL (in)
16
32
MAX.
MEAN
MIN.
1968
Fig.34.
APTERA
M.EUPHORBIAE
M.PERSICAE
AULACORTHUM SOLANI
ALATE
LOG. NO OF APHIDS / 100 PLANTS
4
3
2
1
0
MAY
JUNE
JULY
AUG.

Fig. 35. Proportions of the various nymphal instars in the different samplings of 1968.

Fig. 35 A. 1968

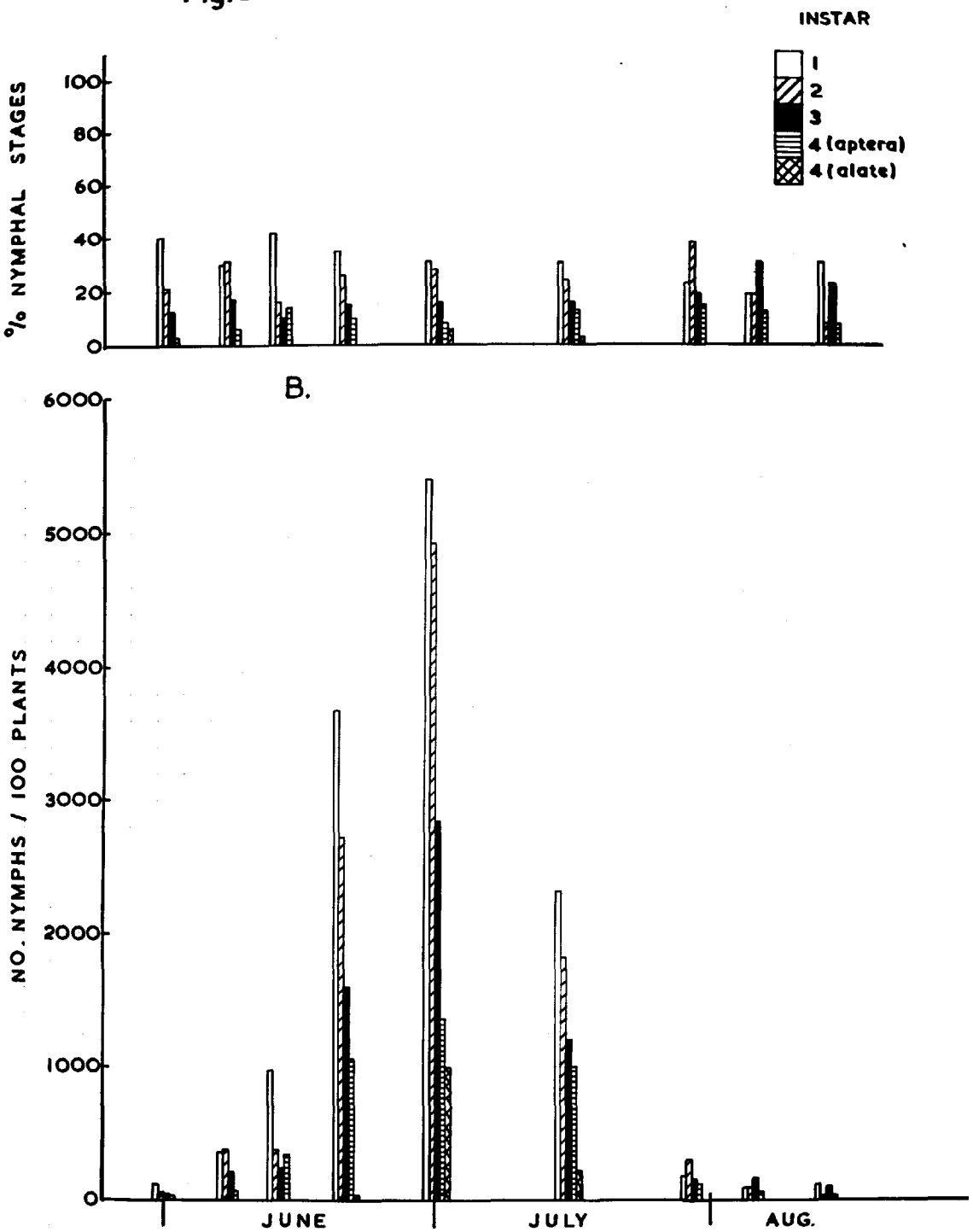

INSTAR
1
2
3
4 (aptera)
4 (alate)
% NYMPHAL STAGES
100
80
60
40
20
0
B.
NO. NYMPHS / 100 PLANTS
6000
5000
4000
3000
2000
1000
0
JUNE
JULY
AUG.

Table 38. Observed and potential populations for each survey of M. persicae on potatoes, 1968.

No.	Date	Calculated potential	Observed	Difference	Observed as % of potential
1	31.5		308		
2	7.6	1500	1210	290	80.7
3	13.6	4430	2355	2075	53.2
4	20.6	17610	10466	7144	59.5
5	30.6	104960	17300	87660	16.5
6	15.7	426880	7500	419380	1.8
7	29.7	137960	780	137180	0.6
8	5.8	3485	480	3005	13.8
9	13.8	4505	390	4115	8.6

(b) Natural enemies.

The 1967 preliminary study made a more detailed investigation possible in 1968. Coccinellids were the first of the natural enemies to appear on the plants (table 39). C. septempunctata was the commonest and the earliest of the 3 species to appear, followed by A. bipunctata and last P. 14- punctata , which was seen wandering as adult on the plant late in the season. Syrphids were detected about mid-June and their number increased during the season and reached a peak by mid-July and then declined afterwards. Species recorded were the same as in the previous year. Anthocorids and chrysopids were recorded sporadically late in the season. Predaceous mites were

Fig. 36. Calculated potential and observed rates of increase of M. persicae on potatoes.

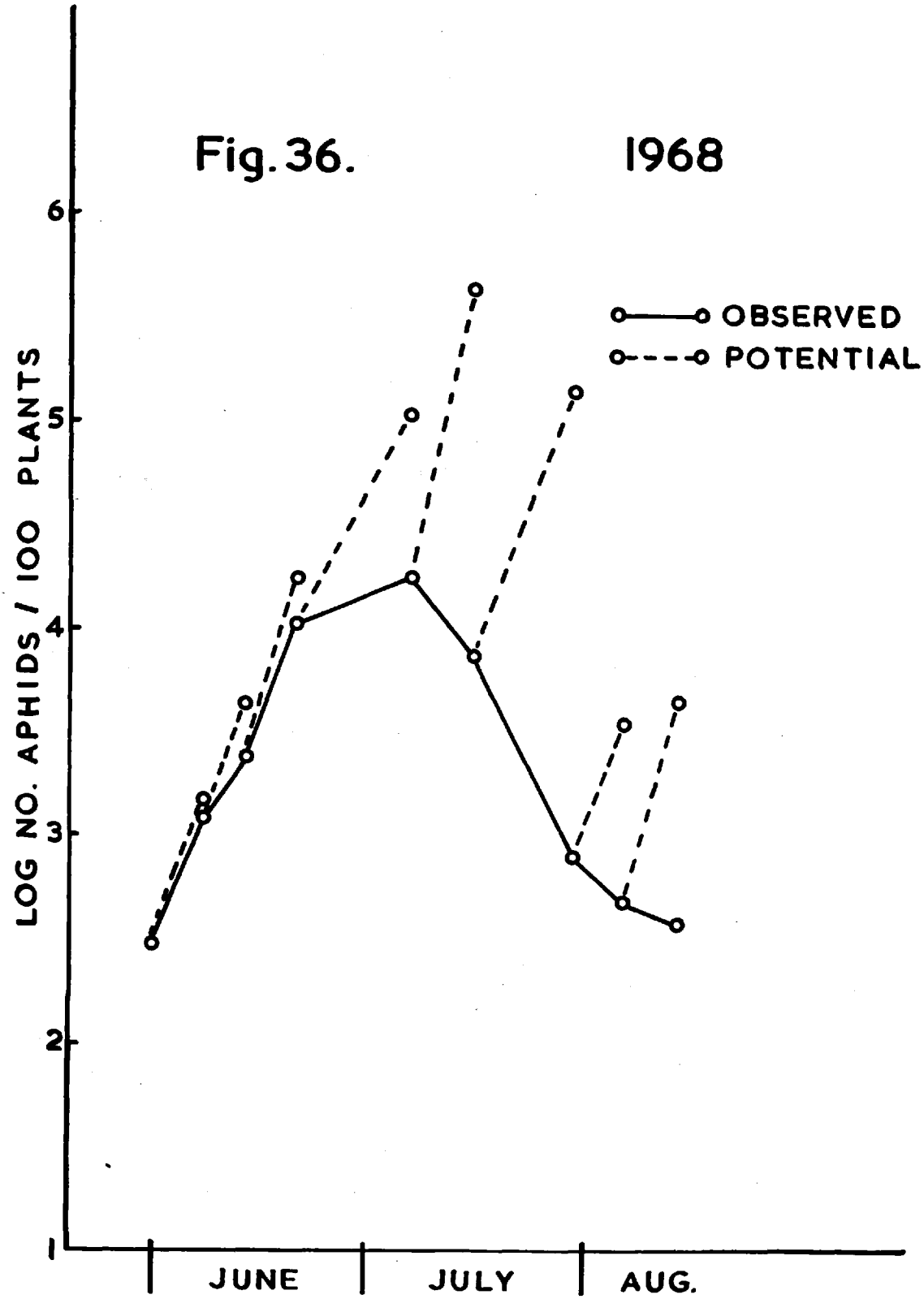


Fig. 36.
1968
OBSERVED
POTENTIAL
LOG NO. APHIDS / 100 PLANTS
6
5
4
3
2
1
JUNE
JULY
AUG.

Table 39. Natural enemies of aphids on 100 potato plants at Silwood Park, 1968.

No.	Date	Infected	Mummies	Anthocorids	Spider mites	Chrysopids	Syrphids	COCCINELLIDS						
								Adults				Eggs	Larvae	Pupae
								*1	2	3	Total			
1	31.5	4(M.e.)	-	-	8	-	-	12	-	-	12	108	-	-
2	7.6	-	-	-	30	-	-	-	-	-	-	210	-	-
3	13.6	5(M.e.)	5(M.p.)	5	5	-	15	-	-	-	-	72	11	-
4	20.6	8(M.e.)	48(M.p.) 16(M.e.) 8(A.s.)	-	8	-	152	-	-	-	-	633	25	-
4	30.6	1560(M.e.)	360(M.p.) 40(M.e.)	-	40	-	200	20	20		40	40	60	-
6	15.7	3325(M.e.)	275(M.p.)	25	-	-	250	-	-	-	-	-	175	50
7	29.7	-	270(M.p.)	-	-	-	150	-	30	-	30	-	-	-
8	5.8	-	60(M.p.)	90	-	30	30	-	-	60	60	-	-	-
9	13.8	-	-	30	-	-	210	-	-	-	-	-	-	-

* 1 Coccinella 7-punctata
2 Adalia bipunctata
3 Propylea 14-punctata

detected in small numbers early in the year and disappeared by the middle of the season.

Parasitized aphids were on the plants by mid-June, the number of mummies increased with the growth of the aphid population reaching their peak late in this month, and decreased afterwards. The species recorded were the same as mentioned before. The parasitized M. persicae (M.p.) outnumbered those of M. euphorbiae (M.e.) and A. solani (A.s.) and in the majority of samplings, mummies collected were exclusively of M. persicae (table 39). Entomophagous fungi attacked aphids as early as the end of May. The infected aphids increased in number with the progress of the season attaining highest numbers by mid-July; no records of them were made afterwards. All infected aphids collected during the samplings were M. euphorbiae.

(c) Trap catches.

The M. persicae and the total number of all aphids collected twice and once a week in water traps and the "Rothamsted survey suction trap" are presented in table 36. Catches of M. persicae in both traps started early in the season and in the water traps they were comparatively higher in the early collections and decreased steadily through the season and then exhibited a slight increase in the 1st week of July (table 36). This coincided with the peak catches in the suction trap. Afterwards the numbers caught decreased in both traps and virtually disappeared by the end of the season.

The suction and water trap data were used to examine the possible effects of some climatic factors on the numbers of alate M. persicae caught. The 3 factors considered were temperature, relative humidity and wind speed. Correlations calculated between the suction and water trap catches and the 3 factors are shown in table 40.

Table 40. Correlation coefficients between M. persicae catches and some climatic factors.

Climatic factors	Water traps	Suction trap
Temperature	+ 0.162 NS	+ 0.397**
Relative humidity	- 0.417**	-0.828***
Wind speed	- 0.132 NS	-0.209 NS

NS - not significant; ** - $p = < 0.01$; *** - $p = < 0.001$.

D. DISCUSSION.

Wide fluctuations in potato aphid populations have been a common feature in most parts of the world (Dunn, 1949; Daiber, 1964; Hadžistevic et al., 1965; Gałecka, 1966; Meier, 1966; Inaizum, 1968). This was attributed to a number of factors among which were climatic conditions, natural enemies and the condition of the host plant. The findings of the present investigations in years 1967 and 1968 agreed in general with the above statement.

(1) Factors influencing the aphid numbers on the potato crop.

(a) 1967 season.

Mac Gillivary and Anderson (1958) studying the population of aphids on potatoes stated that if M. persicae, M. euphorbiae, A. solani and A. nasturtii were released in a field of potato in equal numbers, the density of M. persicae population would become the greatest followed by M. euphorbiae, A. nasturtii and A. solani . Also Barlow (1962) experimenting on the influence of temperature on population growth of M. persicae and M. euphorbiae reported that the innate capacity of increase of M. persicae was higher than that of M. euphorbiae. Results of the samplings presented in table 33 and fig. 31 indicated that M. euphorbiae increased much more quickly than M. persicae and A. nasturtii . According to Barlow and results on page 37 of section II the highest intrinsic rate of increase for M. persicae was at a temperature of 25°C and at 20°C for M. euphorbiae. The discrepancy in numbers of these two aphids in the field could not be explained by the differential influence of temperature which was about 18°C (fig. 31) because the theoretical numbers of M. persicae calculated showed much greater numbers than the observed (table 34). Perhaps the differential effect of natural enemies which are known to be an important deterrent of 'free' progress in development of aphid populations on potatoes (Meier, 1966) was the cause.

The aphidophagous insects recorded early in the season were coccinellid and syrphid predators and parasites. The fact that some aphid species were more suitable food for coccinellids than others was reported by Hodek (1956, 1957). Merritt-Hawkess (1920) stated that Macrosiphum spp. were not acceptable to Adalia species. Blackman (1966) demonstrated that M. persicae and Aulacorthum circumflexum were more suitable for A. bipunctata than some other aphid species. Yakhontov (1966) reported that according to (Saidov, unpublished) syrphid larvae of Scaeva albomaculata, Syrphus corollae, Sphaerophoria scripta receiving a mixture of different aphid species, fed most willingly on M. persicae. These findings coupled with the facts that the % of M. persicae attacked by parasites was much higher than those of M. euphorbiae (table 35) and that the latter was a quick moving insect and is more successful in evading its natural enemies could explain the early check of M. persicae and A. nasturtii population growth relative to that of M. euphorbiae. However, M. euphorbiae showed a sharp drop at the time of the 3rd sampling , which could possibly be the effect of 2 factors. The high maximum temperature of 29°C attained was perhaps more injurious to M. euphorbiae, which is more sensitive to high temperatures than M. persicae (Broadbent and Holling, 1951; Barlow, 1962). The other factor which is seemingly the more important is the effect of rain which was quite heavy on the day of the sampling. This aphid with its habit of colonizing the upper part of the plant and of falling off when disturbed is more vulnerable to rain.

By early July M. persicae and A. nasturtii showed a marked increase when the M. euphorbiae population was decreasing. The steady build-up by the former species was perhaps due to the relatively high maximum temperature which promoted increase and to decreased effect of natural enemies which had become less common (table 35) especially the coccinellids, A. bipunctata and C. septempunctata which are known to be partly mono-voltine and may stop reproducing by end of June (Iperti, 1966). Table 39 which showed that no eggs of coccinellids were found after June confirmed this statement. The interval between 25th July and mid-August marked a period in which the 3 species were surviving as adults in small numbers. This was the period in which parasitism, which is potentially more effective in the control of aphids (van Emden, 1966) reached its peak and could have checked the increase of M. persicae and A. nasturtii. This period also coincided with continuous daily rainfall which suppressed the recovery of M. euphorbiae population.

From mid-August to the end of the season M. euphorbiae underwent its 2nd highest peak followed by a sharp decline, while M. persicae and A. nasturtii showed a slight resurgence. In this period the number of syrphids again increased and some chrysopid, anthocorid and mite predators appeared which checked the growth of M. persicae and A. nasturtii populations, while M. euphorbiae, less affected by these factors and favoured by a dry spell increased rapidly but crashed again following a number of daily rains which were quite heavy (fig. 31 and table 33).

The instar-distributions in table 33 also indicate that M. persicae was checked by natural enemies. The 1st and 4th instar apterae were not recorded in a number of samplings. This was perhaps caused by selective mortalities (Hughes, 1963) i.e. aphidophagous parasites deposited their eggs inside the young nymphs and these were mummified in the 4th instar (Hafez, 1961). That the numbers of the 1st instar nymphs were less than the 2nd in almost all the samplings was possibly due to the former being easier to prey on because of its slow movement, especially by early stages of syrphid larvae. However, the numbers of the 2nd nymphal instars were unexpectedly higher compared with the numbers of the 1st instars from which they originally came.

(b) 1968 season.

Aphid species recorded in 1968 were M. euphorbiae, M. persicae and A. solani. The latter was only recorded in small numbers in the two years. A. nasturtii which was numerous on potato plants in 1967 was not found in 1968. This agreed with Shaw (1955b) who reported that A. nasturtii was not found on potato in some years because of the scarcity on their winter host (Rhamnus sp.).

The trend of the population progress was more simple in 1968 than in 1967. The 3 aphid species steadily increased, M. euphorbiae showing the highest rate. They reached their peaks late in June. The calculated potential numbers of M. persicae (table 38 and fig. 36) showed the difference in the early samplings between the potential

and observed were negligible suggesting that the aphid did not suffer a noticeable check by controlling factors. Later the slow decline of M. persicae populations coincided with increased parasitism which reached its peak by the end of June (table 39); syrphid activity increased and reached maximum by mid-July; also newly appearing anthocorids were possibly contributing to the decline of the population at this time. However, the difference obtained by subtracting the actual from the potential numbers shown in fig. 36 and table 38 could be much bigger than what was actually consumed by the natural enemies because the plants were attacked by blight which possibly reduced the food quality and thus reduced the rate of increase (Shaw, 1955b). Moreover the population was high enough in the middle of the season to initiate intraspecific competition which possibly also decreased the rate of increase (Way, 1966).

(2) Factors governing the density and time of arrival of immigrant alatae.

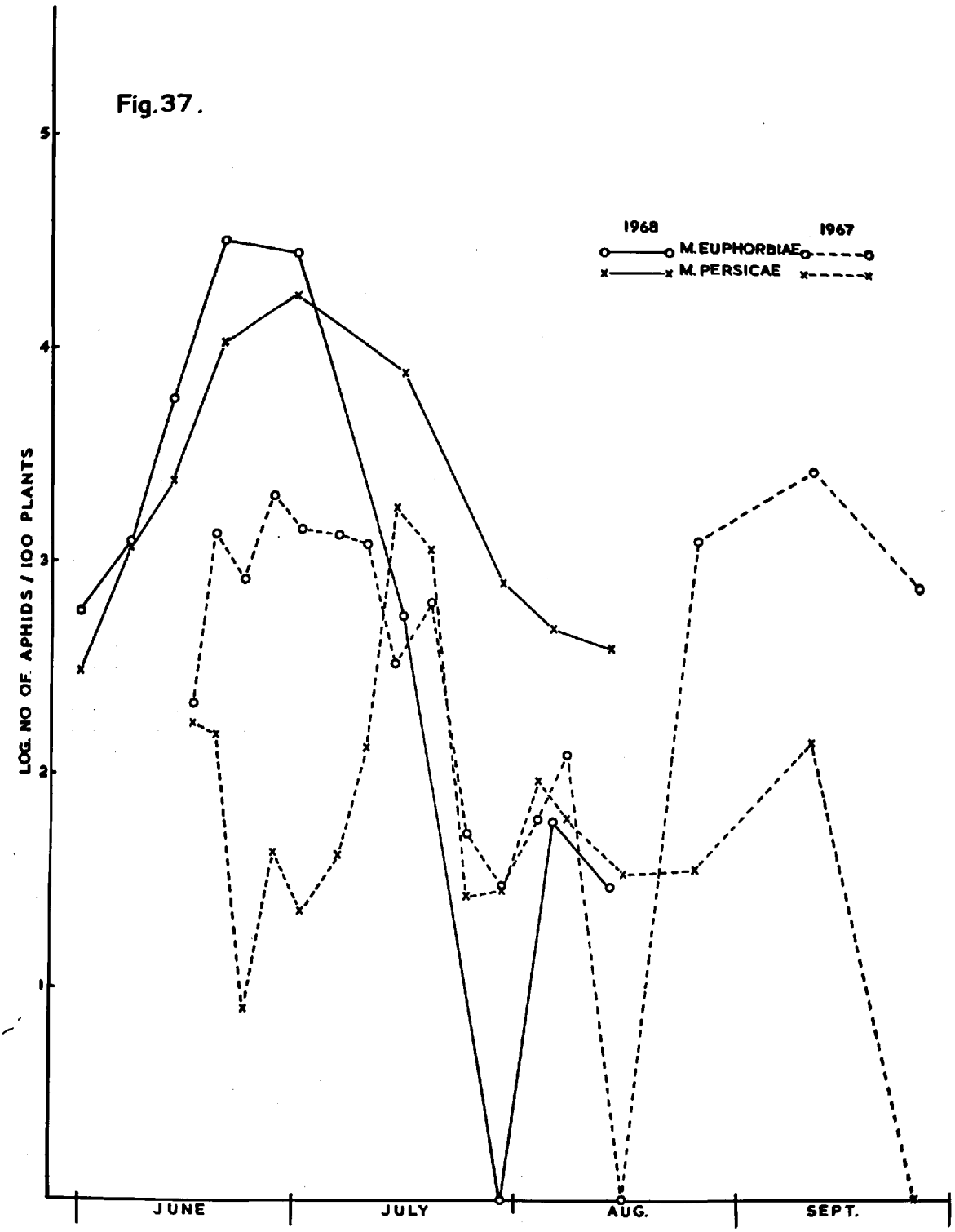
M. euphorbiae and M. persicae are seemingly the two species which are dominant and of regular occurrence on potatoes in this locality. Population fluctuations in each season and the factors possibly governing these are discussed above. However, the considerable differences in densities of aphid populations on potato crops are thought to be partly governed by some factors long before the immigration of alatae to the potato fields. Although

the experimental potatoes were planted on the same date (25th April) in both years, the alatae appeared on the 1968 crop much earlier, there were more, and the aphids started building up on vigorously growing plants long before the time when the 1967 crop was infested by alatae (fig. 37). The density and time of arrival of the alatae on the crop are governed partly by the presence in the vicinity, of overwintering host plants, the most important of which are brassicas for M. persicae (Thomas and Jacob, 1943; Fisken, 1959b). Fisken also reported that M. euphorbiae overwintered as viviparae on strawberry and lettuce, while Thomas and Jacob found it overwintering both as viviparaeand oviparae on strawberry. The number of aphids overwintering as active stages on these hosts depends partly on the severity of the winter.

The other factor is the weather conditions affecting flight to the crop (Johnson, 1954, 1969; Heathcote, 1965). Johnson (1954) concluded that the aerial population of alate aphids was correlated with the number developing on plants and that it was also affected by weather conditions in so far as these influenced the flight activity of alatae. The winter of 1966/7 was milder than that of 1967/8 in which conditions were comparatively unsuitable for aphid multiplication. Nevertheless, the present author collected large numbers of M. persicae in February 1968 (mean minimum temperature -1.2°C) from the buds and heart of brussels sprouts. The abundance of alatae arriving at the crop in 1968 was possibly due to migration from remote areas or to the aphids which persisted on winter hosts

Fig. 37. The relative abundance of M. persicae and M. euphorbiae in 1967 and 1968.

Fig.37.


1968
1967
M. EUPHORBIAE
M. PERSICAE
LOG. NO OF APHIDS / 100 PLANTS
5
4
3
2
1
JUNE
JULY
AUG.
SEPT.

and then multiplied and emigrated early in the favourable weather conditions which prevailed in the 2nd half of May, 1968. By contrast the weather in May, 1967 was wetter and the maximum temperatures for the last week of this month were much lower than in 1968.

Another hypothesis suggested by Meier (1966) to explain a heavy infestation following a low one was that when the aphid population was low on the potato crop, especially late in the season the multiplication of the natural enemies is restricted by scarcity of food and they tend to occur in small numbers in the following year and consequently have little effect in suppressing the aphid build-up in the early part of that year. It seems that in 1968 the late appearance of the natural enemies on the crop was also important as well as their comparative scarcity, because the aphids had multiplied before the enemies came in significant numbers This was perhaps promoted by a comparatively lower temperature early in the 1968 season which favoured the aphid more than its natural enemies (Dunn, 1952; Hodek et al, 1966). Van Emden (1966b) discussed the effectiveness of natural enemies in controlling aphid population. Among other factors he emphasized the importance of synchronization of the appearance of the natural enemies with their prey, and using Bombosch's (1963) model he calculated the effect of varying the delay in the appearance of natural enemies.

(3.) The effect of weather factors on movement and flight of alate aphids.

Catches of alatae among the crops ~~of alate aphids~~ using Moericke type (1951) water traps in 1967 and 1968 (table 36) correlate in general with the results of the samplings of the potato plots. The 1967 counts on plants showed the 1st peak early in the season when immigrant alatae were colonizing the plants and a 2nd one by mid-July (table 33). In the same year the water trap catches early in the season were small and inconsistent, but reached a peak in mid-July caused by alatae produced on the crop which showed the 2nd peak. In 1967 alatae arrived relatively late on the crop and perhaps due to age, muscle autolysis (Johnson, 1953) or undergoing a number of migratory flights before arriving in the experimental potatoes, they perhaps settled quickly on the plants and were not caught in traps during trivial flights from plant to plant.

In 1968 the 1st catch of M. persicae in water traps was larger than the second which was a remarkably small one. The alatae arrived on the crop relatively early and perhaps tended to leave the plants and fly off again (Kennedy, 1950) and so did not settle as in 1967. Such 2nd flights are sometimes preceded by short flights from plant to plant which might have resulted in the high 1st catch (Johnson, 1954). However, the 2nd catch may have been decreased by a wet period of 3 days rainfall and low temperature (fig. 34).

The water trap catches in the middle of the season (July) were much higher in 1967 than 1968, although the numbers counted on

the plants showed the opposite trend (tables 33 & 37). The tendency for alatae produced on the crop is to emigrate after moulting and since weather conditions for flight were more favourable in 1968 than in 1967, less aphids were caught in the water traps in the former year though this coincided with the maximum catch in the suction trap. It can be concluded that catches in water traps are influenced by the amount of plant to plant flight in the crop as well as by the number of immigrant alatae whereas catches in the 'Rothamsted Suction trap' reflect immigrant and emigrant numbers and are not influenced by what is happening among plants in a crop.

The 1968 M. persicae catches in the Rothamsted survey suction trap were relatively large early in the season, then declined and rose to a maximum in the 1st week of July. Catches then decreased steadily to the end of the season (table 36). The early large catches perhaps coincided with the period in which M. persicae left their parent host plant on which they overwintered and were emigrating to the summer hosts. Their numbers in the trap were influenced by the level of population on these winter hosts and also the climatic conditions which were favourable for flight. The 2nd peak coincided with the abundant alatae produced on potatoes and perhaps on other summer hosts and which took to wing soon after maturation, assisted by prevailing relatively low wind speeds (5.5 m/h), low relative humidities (73%) and a mean temperature of about 15°C.

M. persicae catches in the water and suction traps correlated with 3 climatic factors (table 40). There was a positive

correlation with temperature and negative with relative humidity and wind speed. Generally there were better correlations of the 3 factors with the suction trap catches. However, relative humidity seems to be more important than temperature and wind speed in governing water trap catches. These results agree basically with the findings of many investigators (Davies, 1935, 1936, 1939; Davies and Whitehead, 1935; Loughnane, 1944). However, Kareem and Basheer (1966) reported a positive correlation with relative humidity and a negative correlation with temperature, which contradicted the results of the present work and those of the above authors. Kareem and Basheer worked in India at temperatures ranging from a mean minimum of 19°C to a mean maximum of 32.2°C. It is possible that temperatures were too high i.e. above the upper threshold for aphid flight. If follows that the positive correlation of aphid catches with temperature which prevails in temperate climates would not necessarily apply to conditions in India. Their statement that maximum number was trapped at the lowest mean minimum temperature confirms this.

SECTION V ASSESSMENT OF THE EFFICIENCY OF APHIDOPHAGOUS INSECTS IN THE FIELD BY EXCLUSION METHODS.

A. INTRODUCTION.

The fact that insecticidal application for the control of insect pests resulted in resistant strains was 1st noticed in 1914 by Melander who reported that the scale insect, Aspidiotus perniciosus had gained resistance to lime sulphur. Other similar observations were reported by a number of investigators who also noticed that the insect did not only acquire resistance to the particular chemical with which it was treated, but was sometimes difficult to control with other insecticides. However, this was not the only hazard of chemical applications because as a result of their continuous application, other insects which were only found in small numbers multiplied rapidly and shot to a pest level. This was postulated to be the effect of these chemicals destroying their natural enemies which kept them under check. Steiner and others (1944) observed that applications of DDT against codling moth on apples resulted in a sudden rise of the red mite populations. This necessitated the search for a selective insecticide which ideally kills the pest and leaves out its natural enemies (Ripper, 1944).

That biological agencies in nature suppress insect increase is a widely accepted view, but the magnitude and the scientific proof

of the control are lacking. De Bach (1946), De Bach et al. (1949, 1951) and Fleschner et al. (1955) working in California tried a sequence of techniques and proved convincingly that natural enemies were responsible for controlling some insect pest populations. Sailer (1966) estimated the effect of natural enemies on the potato aphid, Macrosiphum euphorbiae by caging a number of them on potato plants and thus excluded their enemies. An equal area outside the cage was infested with the same number of aphids, but the aphidophagous insects were left undisturbed. After a month the plants inside had nearly collapsed under the heavy infestation of the aphid, while outside the cage no injury was apparent. Bombosch & Tokmakoğlu (1966) also used the caging technique with Aphis fabae and concluded that in one experiment the increase in number of A. fabae inside the cage was about 360 fold of that outside the cage which was normally attacked by the natural enemies.

Evidence from a number of experiments showing the injurious effects of insecticides on aphidophagous insects initiated further studies to estimate the efficiency of these enemies in suppressing the aphid population using chemical check methods. Way (1949) used DDT and BHC to elucidate their effect on the natural enemies of M. persicae and to estimate their controlling efficiency. Meier (1966) tested a number of insecticides on the natural enemies of potato aphids and concluded that when insecticides causing high percentages of kill of enemies were applied, the aphid numbers

increased rapidly especially when the insecticide was not very effective against the aphids.

The present work aimed at estimating the efficiency of the natural enemies of M. persicae in the field on potatoes and brussels sprouts using exclusion techniques by caging and also a preliminary trial using an insecticide.

B. MATERIALSAND METHODS.

Experiments were done in 1967 and 1968 on potatoes and brussels sprouts. These were conducted on the same potato plots as described on page 146 and during the period when the samples were taken to assess the field populations of aphids and their natural enemies. The brussels sprouts plots of about 50 x 30 m. in area were adjacent to the potato plots. Experiments on the former were started in late September and mid-August in 1967 and 1968 respectively and comprised 5 treatments and a control, each replicated 3 times. All cages were 2'6" x 2'6" x 4'6". The treatments were as follows (plate 3):

1) Cages were covered all round and on the tops with terylene net (mesh size = 1 x $\frac{1mm}{2}$) to exclude all natural enemies of aphids including birds. A roof of 6' x 6' wooden frame with wire netting as a support and polythene sheet fixed on the top were placed on the top of these cages to exclude rain. The large overlapping roofs were to minimize the effect of wind drift of the rain.

Plate 3 - Caging experiment. The various treatments on brussels sprouts.

2- The same treatment as 1 except a cellulose acetate sheet covered with an adhesive glue was fixed to the top from the inside to trap alatae leaving the plants and wandering inside the cage.

3- Cages were covered all round with trylene and with ½" mesh netting on the tops. This allowed almost a normal rainfall on the plants and also allowed alatae to disperse from the top. A cellulose acetate strip of about 2" was pinned to the outer upper most part of the cages and plastered with glue to trap natural enemies crawling up the cage to enter through the string netting.

4- Cages were covered with ½" netting to allow free movement of insect natural enemies, but not birds.

5- Only the wooden frames without covering; but roofs described under 1 were placed on the tops to exclude rain.

6- Control - uncaged.

(1) Caging experiments.

18 plants were selected from the potato plot and sprayed with nicotine to destroy all aphids and were searched thoroughly for natural enemies which were removed. 3 plants were taken at random for each treatment and the soil around the ones from which natural enemies were to be excluded were dusted with dieldrin to kill soil predators. Newly emerging M. persicae adults developed on brussels sprouts in 20°C environment controlled room were transferred to these plants. 10 of these were sleeved on to a young stem of each plant and another 10 to an old stem for about 2 days for them to settle before the sleeves were carefully removed. In the period when the sleeves

were on, the 3 replicates of each treatment were chosen at random, and the appropriate cages were transferred to cover the plants. The cages were fixed to the ground using pegs at their bases and also wire strings from the tops especially the ones with roofs, so that they were not blown away by wind. The plants were again inspected and all aphids and natural enemies were destroyed before the sleeves were removed.

Aphids were counted directly after the removal of the sleeves and a number of early counts followed at short intervals of about 3 days, which were later prolonged to a week or 10 days. Natural enemies were counted without disturbance in treatments 4-6, but also in treatments 1-3 the few enemies encountered were counted and removed. In the 1967 experiments on potatoes, the aphids after 10 days on control plants and shortly afterwards on treatment 4 completely disappeared and were then replaced as before. When the aphid populations were high in treatments 1 and 2 and mortality due to pathogenic fungus set in, the experiments were terminated and the cages were transferred to brussels sprouts and experiments repeated following the same procedure as described above.

Temperature data were obtained from the thermograph mentioned in section IV. This was also transferred with the cages to the brussels sprouts plot and the measuring probe placed under a leaf. A hygrograph was fixed in an open cage and another in a trylene netted one to measure differences in relative humidities.

(2) Insecticidal check method.

15 brussels sprout plants, nearly of the same size and vigour were selected. These were divided randomly into 2 treatments and a control, each with 5 replicates. The lay out was as follows;

1- Plants were treated with 0.5% sevin using a hand operated sprayer giving large droplets of the liquid. This was directed to the buttons and hearts of the plants to kill natural enemies hidden in these parts and also the ones crawling up the main stem from the soil. The upper surfaces of the leaves were carefully sprayed mainly against adult parasites which normally landed on the upper surfaces and wandered to find their prey. The under surfaces of the leaves bearing the aphids were not sprayed. Coccinellids were generally scarce in August and were seldom seen on brussels sprouts. Syrphids which were the most abundant predators (Way et al., 1969) were eliminated by removing all eggs on alternate days. Thus these plants were considered 'natural enemy-free'.

2- Plants were inspected on alternate days and syrphid eggs were removed. Other natural enemies were undisturbed. The difference between 1 and 2 accounted for the effect of natural enemies other than syrphids.

3- Control - received no chemical treatment and all predators were allowed to increase normally on the plants.

The oldest leaves hanging on the ground were removed from the 15 plants and they were sprayed and allowed to dry before the aphids

were sleeved. 10 young adult M. persicae cultured on brussels sprouts in the 20°C environment controlled room were sleeved on a mature leaf. The plants were examined and all natural enemies on 'natural enemy-free' plants were destroyed. The sleeves were removed after 2 days and the aphids counted. A number of counts were made first at short intervals, which were later prolonged. Syrphid eggs were counted and removed on alternate days from plants of treatment 1 and 2. All natural enemies found on treatment 1 plants were destroyed whenever found. Another application of the insecticide was made after a fortnight.

C. RESULTS.

(1) Caging experiments.

(a) 1967.

Tables 41 and 42 show the various groups of natural enemies which attacked aphids on the experimental potatoes and brussels sprouts. Parasites and syrphids occurred regularly and were apparently the main natural enemies affecting aphid increase. Coccinellids and anthocorids were found on potatoes but brussels sprouts were virtually free from them. On potatoes numbers of anthocorids increased towards the end of the season. Results also show that treatments NO. 1, 2 and 3 which were supposed to be free of natural enemies supported varying numbers of these, especially parasites as indicated by aphid mummies. It is possible that these natural controlling

agents were attracted by the high number of aphids inside these cages (Sailer, 1966) and some were induced to oviposit on the cages whereas a few parasites probably entered through the netting or the cage door.

Experiments on potato plants.

Numbers of M. persicae steadily increased almost at the same rate (fig. 38) in cages which were 'natural enemy-free' and rain was kept out (treatment 1 & 2). The small discrepancies were possibly caused by the varying small numbers of natural enemies found in these cages. Elimination of alatae by sticky tops did not seem to affect the population progress. The numbers in cages which were 'natural enemy-free' but rain not excluded increased at a relatively slower rate than the previous treatments. This was perhaps because relatively more natural enemies entered these cages particularly towards the end of the experiment in which their numbers increased (table 41), or perhaps rain had directly destroyed some aphids. In cages with string netting all round, aphids maintained their initial numbers until the first count, but fell sharply afterwards following an increase in natural enemies and heavy rains. 20 young adults were again transferred to each plant of this treatment (shown by an arrow in fig. 38) when the aphids inside were eliminated. Aphids in cages protected only from rain showed a steady decrease throughout the experiment. The controls underwent a very sharp decrease and the aphids had disappeared by the time of the 1st count. 20 young adults

were again transferred on 15th August (shown by an arrow) and had again disappeared by the end of the experiment.

Table 41. Numbers of aphids and natural enemies per three potato plants in the various cage treatments in 1967.

Date	No. of Aphids and natural enemies	Treatments *1	2	3	4	5	6
10.8	Aphid mummies	6	8	11	3	5	2
	Coccinellids	-	1	2	3	4	-
	Anthocorids	-	-	-	-	4	2
	Mites	-	-	-	-	3	1
	Aphids	379	430	288	66	66	0
20.8	Aphid mummies	8	5	2	2	5	1
	Anthocorids	-	2	-	7	5	2
	Mites	-	1	2	2	2	-
	Aphids	2089	973	614	2	52	9
30.8	Aphid mummies	9	12	1	1	1	2
	Syrphids	-	-	-	19	15	15
	Anthocorids	3	-	4	1	1	-
	Mites	-	1	1	-	-	-
	Aphids	10399	3881	4257	19	10	8
10.9	Aphid mummies	29	1	21	2	1	1
	Syrphids	6	2	6	12	10	4
	Coccinellids	-	-	2	2	-	-
	Anthocorids	4	3	4	13	2	-
	Mites	-	-	4	9	4	1
	Aphids	17251	10539	938	34	5	0

* Treatment 1. Trylene all round + Polythene tops.

2. As (1) + sticky tops for alatae collection.

3. Trylene all round + string netting on tops.

4. String netting all round and tops.

5. Polythene tops only.

6. Control.

Fig. 38. Numbers of M. persicae per potato plant in the various cage treatments in 1967.

1 ● ——— ● calculated potential increase.
2 △ ——— △ trylene net all round + Polythene tops.
3 △ - - - △ as (2) + sticky tops for alatae collection.
4 0 ——— 0 trylene all round + string netting on tops.
5 0 - - - 0 string netting all round and tops.
6 X ——— X polythene tops only.
7 X - - - X uncaged control.

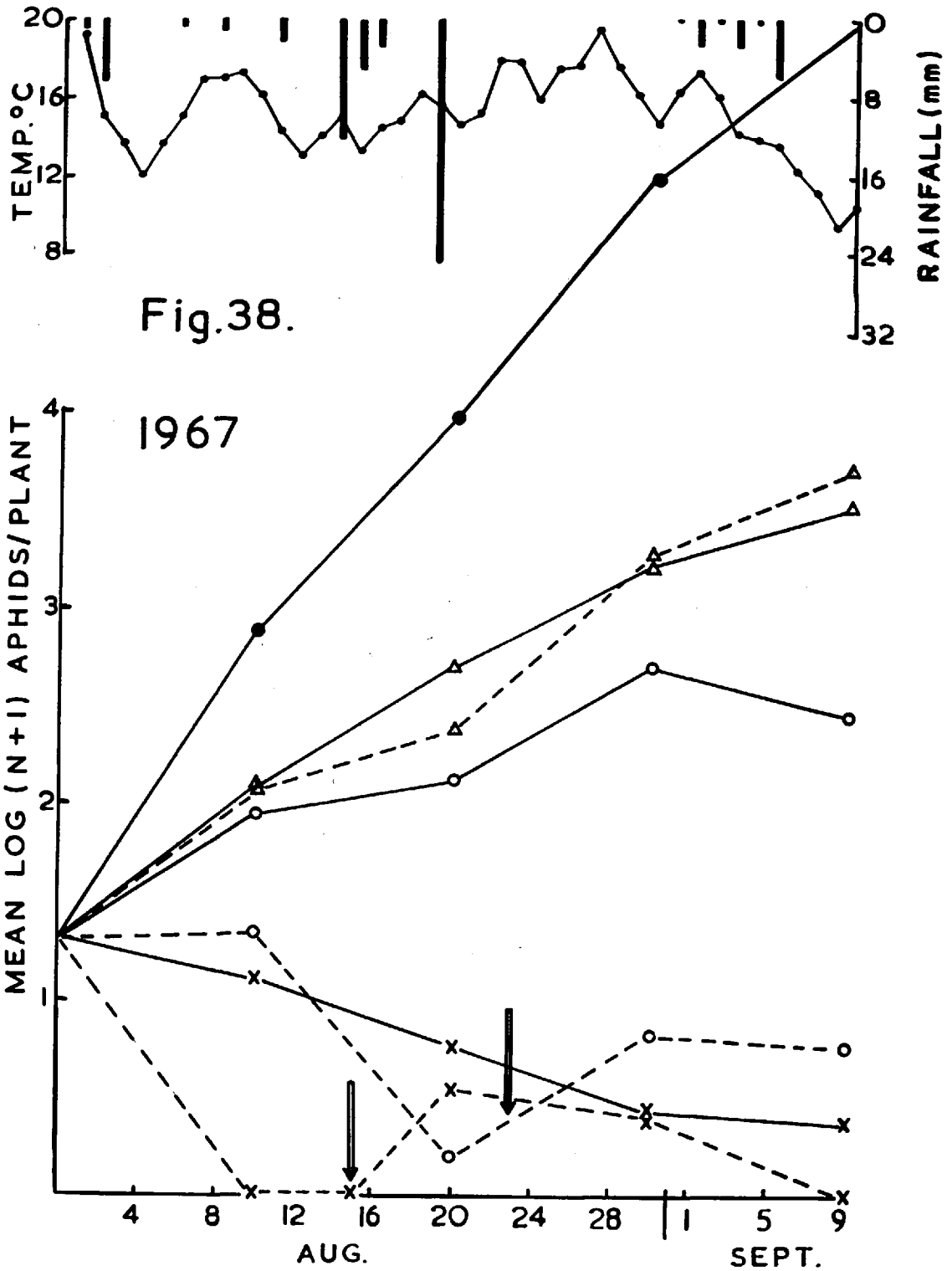

TEMP. °C
20
16
12
8
0
8
16
24
32
RAINFALL (mm)
1967
MEAN LOG (N+1) APHIDS/PLANT
4
3
2
1
4
8
12
16
20
24
28
1
5
9
AUG.
SEPT.

Fig.38.

Table 42. Numbers of aphids and natural enemies per three brussels sprout plants in the various cage treatments in 1967.

Date	No. of Aphids and natural enemies	Treatments 1	2	3	4	5	6
2.10	- Aphids	206	239	198	234	286	340
4.10	Aphid mummies	-	-	2	2	4	-
	Syrphids	-	1	-	2	-	5
	Mites	-	1	-	1	2	-
	Aphids	215	215	187	257	214	194
10.10	Aphid mummies	1	3	8	4	2	1
	Syrphids	-	-	-	1	-	3
	Mites	2	-	2	1	-	-
	Aphids	398	382	407	409	341	117
18.10	Aphid mummies	-	-	-	1	1	-
	Syrphids	-	-	2	2	-	5
	Mites	1	3	2	1	-	2
	Aphids	551	493	353	445	416	71
2.11	Aphid mummies	4	4	4	1	4	-
	Syrphids	-	-	-	1	-	-
	Mites	4	3	-	1	2	-
	Aphids	1847	1105	1061	736	1075	37
18.11	Aphid mummies	4	11	2	6	3	-
	Mites	2	1	-	-	2	-
	Aphids	2088	1310	1100	940	524	32

Experiments on brussels sprout plants.

Rates of population increase under the 1st. 5 treatments did not show marked differences (fig. 39). This was perhaps due to the small numbers of natural controlling agents recorded in this period (table 42), the activity of which was checked by the low temperatures which prevailed during most of the period of the experiment (fig. 39). However, aphids on plants protected only from rains showed a decrease

Fig. 39 Numbers of *M. persicae* per brussels sprout plant in the various cage treatments in 1967.

1 ● ——— ● calculated potential increase.
2 △ ——— △ trylene net all round + Polythene tops.
3 △ - - - △ as (2) + sticky tops for alatae collection.
4 0 ——— 0 trylene all round + string netting on tops.
5 0 - - - 0 string netting all round and tops.
6 X ——— X polythene tops only.
7 X - - - X uncaged control.

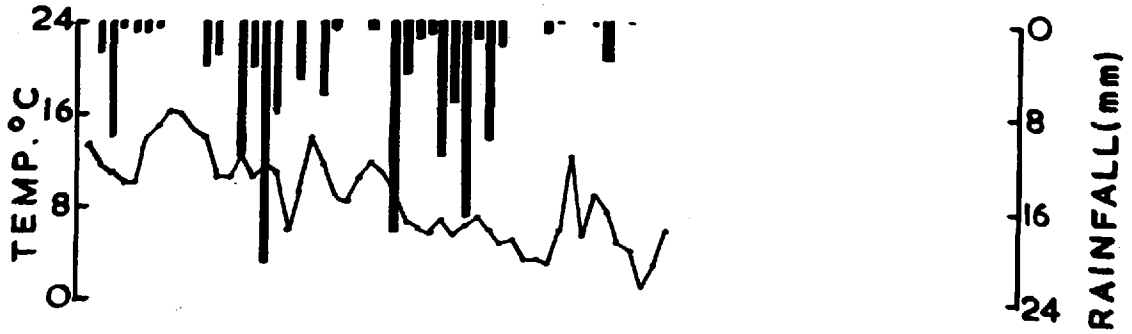
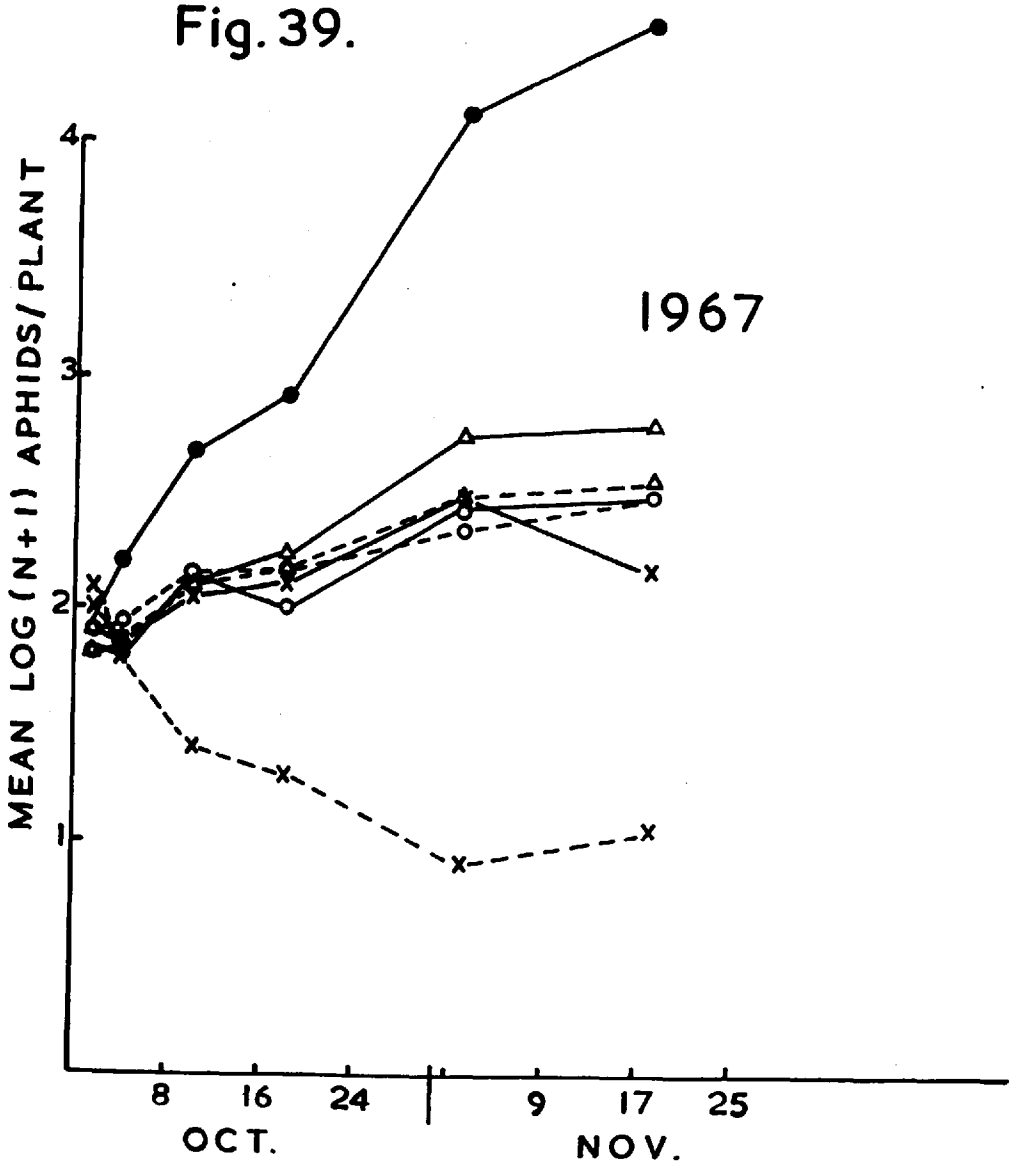

24
16
8
0
TEMP. °C
0
8
16
24
RAINFALL(mm)

Fig. 39.


MEAN LOG (N+1) APHIDS/PLANT
4
3
2
1
1967
8
16
24
OCT.
9
17
25
NOV.

in the last count. Numbers on control plants steadily decreased and exhibited a marked difference compared with the other treatments. This was possibly due to the effect of birds which may have been deterred by the caging even if consisting of an open frame.

(b) 1968.

Table 43 shows the natural enemies encountered during the counts on brussels sprouts of which parasites and syrphids were the dominant ones. Coccinellids and anthocorids were scarce and were recorded only once during the experiment. Some enemies were also recorded on the 'natural enemy-free' cages, especially parasites which resulted in large numbers of aphid mummies.

Aphid populations in the 'natural enemy-free' cages steadily increased, although in cages in which rain was allowed, the rate of increase in the last count was slightly slower than in treatments 1 and 2. In cages with $\frac{1}{2}$" netting all round and those with tops to exclude rain, the rate was inconsistent and underwent a number of rises and falls but was higher than the control which steadily decreased throughout the experiment (fig. 40). This difference perhaps reflected the effects of birds which did not enter cages even when open.

(2) Insecticidal check method.

Figs. 41 and 42 show the trend of changes in numbers of M. persicae and syrphid eggs on brussels sprout plants in 1968 and 1969 respectively. The rate of aphid population increase on plants sprayed with sevin and

with syrphid eggs removed was the highest and showed increase in all counts except one in each year. On 'syrphid-free' and control plants there was no clear difference; numbers remained few throughout and although in 1968 there were more on the 'syrphid-free' plants initially there were less in the last count. In 1969 the numbers on 'syrphid-free' plants was lower than on the controls in the first half of the experimental period, but higher in the second half. Syrphid eggs were more abundant in 1969 than 1968 and each year they were more prevalent in the 1st. half of the experimental period.

Table 43. Numbers of aphids and natural enemies per three brussels sprout plants in the various cage treatments in 1968.

Date	Aphids and natural enemies	Treatments 1	2	3	4	5	6
12.8	- Aphids	303	266	283	295	282	269
15.8	Aphid mummies	-	1	-	-	2	-
	Syrphids	-	-	-	3	4	3
	Aphids	516	406	456	357	350	296
21.8	Aphid mummies	3	1	-	2	8	2
	Syrphids	-	1	1	3	14	13
	Coccinellids	-	-	-	-	1	-
	Mites	1	1	-	-	1	-
	Aphids	691	628	593	330	274	222
3.9	Aphid mummies	105	95	35	30	40	25
	Syrphids	2	-	-	2	32	21
	Mite	-	-	-	-	2	-
	Aphids	5180	4195	3202	694	344	191
12.9	Aphid mummies	-	-	-	11	17	12
	Syrphids	-	-	-	-	13	7
	Mite	-	-	-	2	-	3
	Aphids	13298	11152	12138	2469	1254	242
27.9	Aphid mummies	-	-	-	8	8	7
	Syrphids	-	-	-	17	19	29
	Anthocorids	-	-	-	-	-	2
	Mites	-	-	-	3	2	-
	Aphids	36285	30872	18815	636	1240	67

D. DISCUSSION

The experiments on potatoes and brussels sprout plants showed that *M. persicae* protected from natural enemies increased more than when natural enemies had free access. The numbers inside the 'natural enemy-free' cages (treatments 1, 2 & 3) increased at about the same rate especially on brussels sprouts on which aphids are less affected

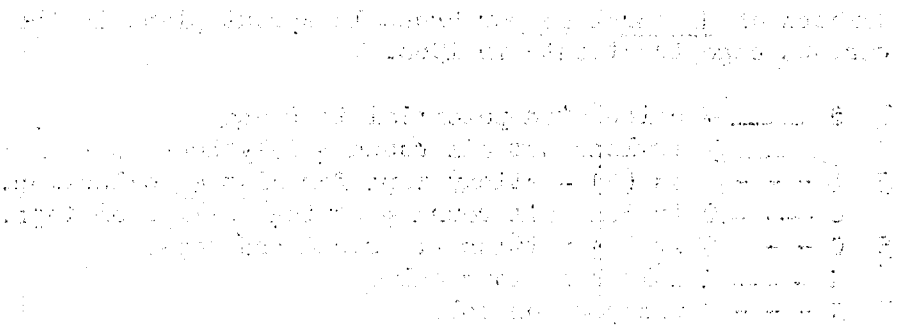
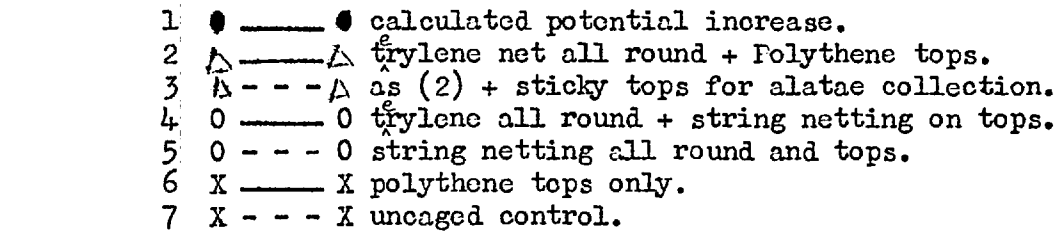


Fig. 40. Numbers of *M. persicae* per brussels sprout plant in the various cage treatments in 1968.



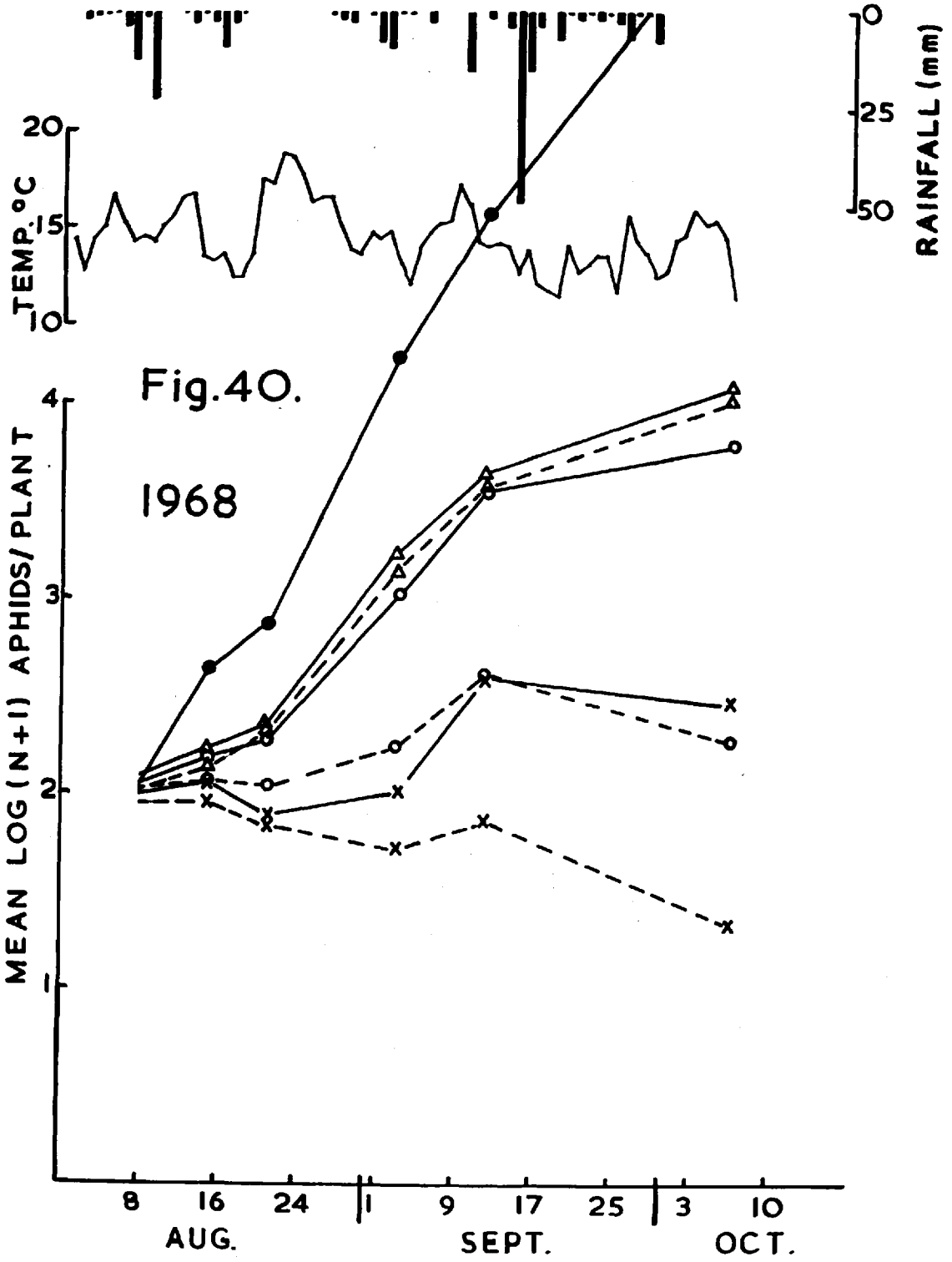

RAINFALL (mm)
0
25
50
TEMP. °C
20
15
10
MEAN LOG (N+1) APHIDS/PLANT
4
3
2
1
8
16
24
1
9
17
25
3
10
AUG.
SEPT.
OCT.

Fig.40.

1968

Fig. 41. Mean numbers per plant of M. persicae and syrphid eggs in 1968.

0 -.-.- 0 treated and syrphid eggs removed.
0 - - - 0 syrphid eggs removed.
0 _____ 0 control.

Fig.41. A. 1968

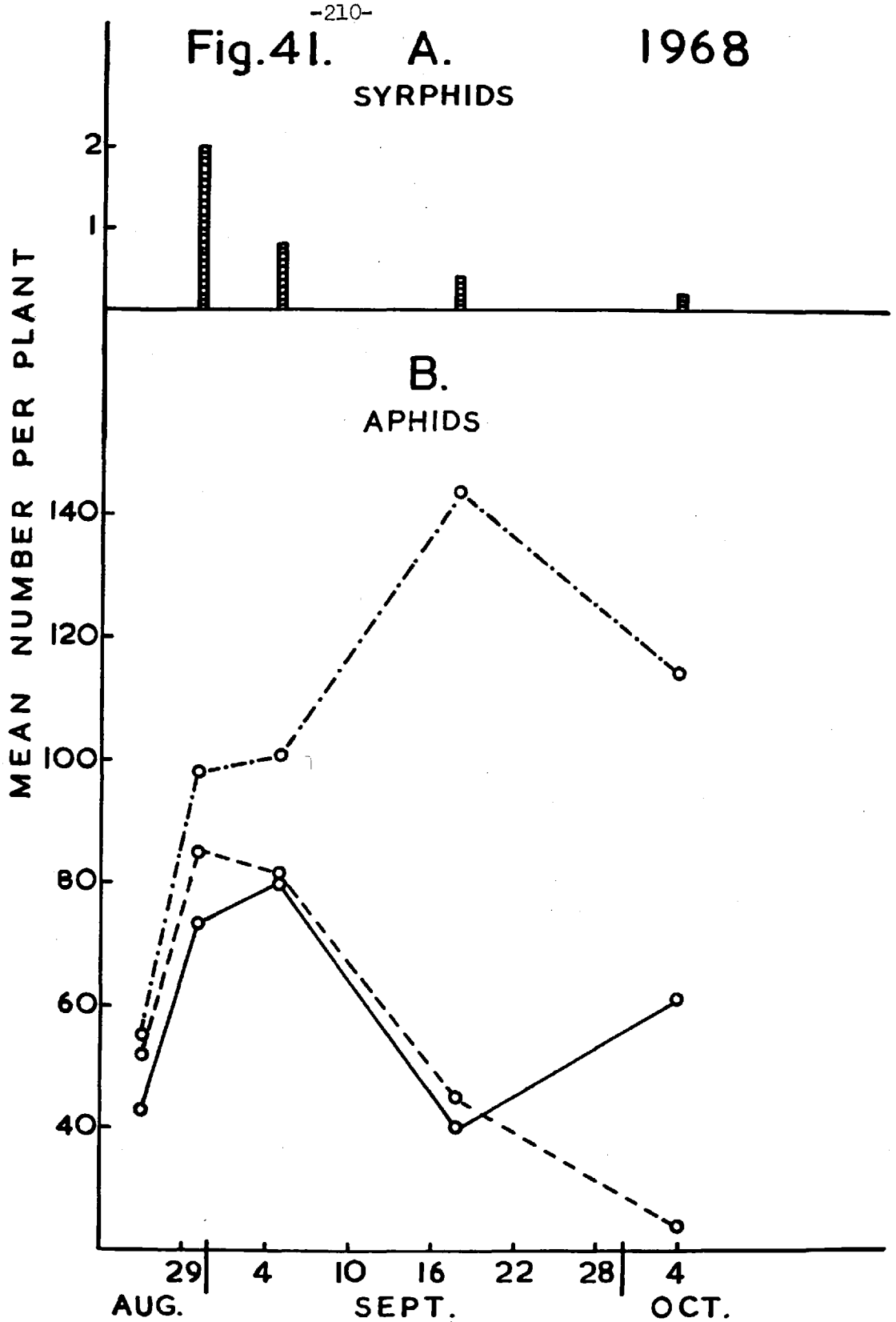

SYRPHIDS
2
1
B.
APHIDS
MEAN NUMBER PER PLANT
140
120
100
80
60
40
29
4
10
16
22
28
4
AUG.
SEPT.
OCT.

Fig. 42. Mean numbers per plant of M. persicae and syrphid eggs in 1969.

● _____ ● calculated potential increase.
0 -•-•- 0 treated and syrphid eggs removed.
0 - - - 0 syrphid eggs removed.
0 _____ 0 control.

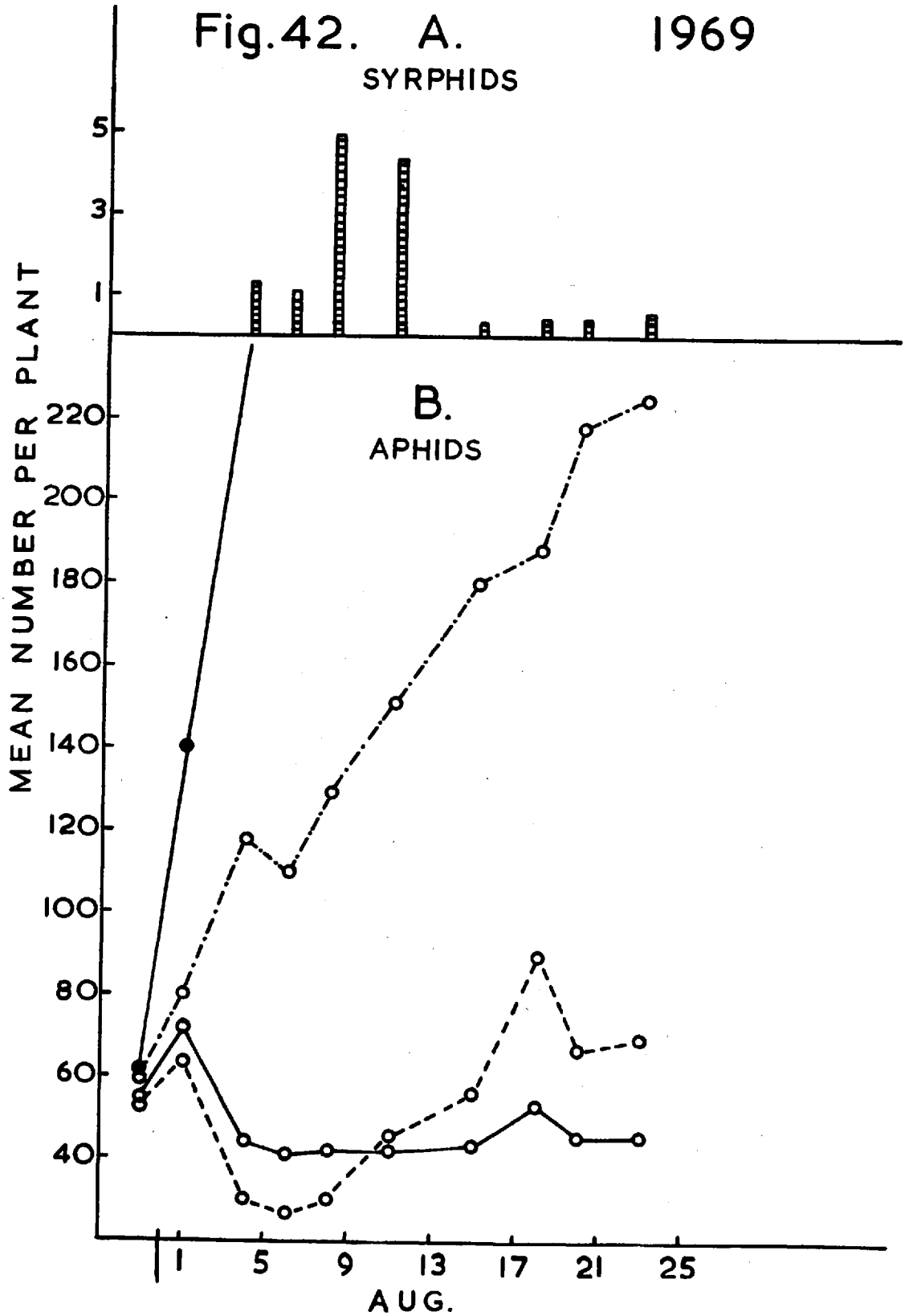


Fig.42. A. 1969
SYRPHIDS
5
3
1
B.
APHIDS
MEAN NUMBER PER PLANT
220
200
180
160
140
120
100
80
60
40
1
5
9
13
17
21
25
AUG.

by rain (figs.39 & 40). However, on potatoes the aphids seemed to be more vulnerable to rain, and thus showed a slightly lower rate of increase (fig. 38). In treatments 4, 5 and the control where the aphids were attacked by natural enemies, the numbers were much less particularly on the controls. The check by natural enemies seemed to be greater on potatoes than on brussels sprouts, perhaps because the former is visited by a larger group of natural enemies. Coccinellids and anthocorids which were seen actively searching potato plants and perhaps of major importance in reducing aphids were only recorded once on single brussels sprout plants (table 43). However, in October and November when the experiments with brussels were done the effect of aphidophagous insects may be less important than in summer when the experiments with potatoes were done (fig. 38). This could be attributed to their small numbers (table 42) and to retardation of their activity by the lower temperatures (Dunn, 1952). Birds preying on aphids seem to be more important at this time. However, the rate of increase of the aphids was also slow due to the low temperatures.

M. persicae populations in the 'natural enemy-free' cages were perhaps modified by the number of the aphidophagous insects which were found there, especially by parasitism which was high in some counts. The effect of these and other natural enemies could be minimized by counts at shorter intervals. Cages with string netting all round which were supposed to allow free movement of all insect natural enemies may not have done so, particularly with syrphids which hover over the plant

before landing on it. Table 43 which indicates many more syrphids in open cages and on the controls confirms this. Also in cages where a population of aphids built up and an amount of honey-dew was excreted, some ants were attracted to it and perhaps affected the rate of increase by protecting the aphids (De Bach et al., 1951). In the later counts the aphid populations, especially in the 'natural enemy-free', became very large and they no doubt initiated intra-specific competition which would affect the quality and multiplication rate of the individuals.

Aphid populations on brussels sprouts sprayed with 0.5% sevin and with syrphid eggs removed by hand on alternate days showed remarkably greater numbers than those on the controls and 'syrphid-free' plants (figs. 41 & 42). This is seemingly due to the elimination of important natural enemies, other than syrphids. In 1968 the aphid numbers on plants from whioh only syrphid eggs were removed remained almost similar to those on control plants for all the oounts except the last one when there were less. In 1969 counts, the populations on these plants were less than on controls for the 1st half of August, although in this period the maximum numbers of syrphid eggs were removed from the plants. In the 2nd half of August the aphid numbers increased and were slightly higher than on the control, although syrphid eggs in this period were fewer. This indicates that although syrphid eggs were on the plants as potentially important aphid predators, they failed to exercise any effective control measure on the aphids. This agrees with Way et al. (1969) findings who recorded a similar

result with Brevicoryne brassicae on brussels sprouts. They attributed this to an unexplained phenomenon of large loss of newly hatched larvae.

The difference between aphid populations on 'syrphid-free' and 'natural enemy-free' plants were high and is the result of all natural enemies other than syrphids. The main aphidophagous insects recorded on the brussels sprouts were parasites, syrphids and few predaceous mites. Since syrphids were removed and parasites were quite few on the plants, it must be assumed that most of the control was exercised by unknown predators; perhaps from the soil e.g. staphylinids and carabids.

Aphid populations on 'natural enemy-free' plants increased at a much slower rate than the calculated potential (figs. 38, 39, 40 & 42). This reduction in numbers and slower rate of multiplication in experiments with insecticidal check method were perhaps caused by rain, birds preying on the aphids and or sevin reducing the reproductive rate of M. persicae (Bovey et al., 1962). However, much of the difference is probably caused by a higher mortality under crowded conditions, decreased reproductive rate and perhaps nutritional factors related to the changing quality of host plant.

SECTION VI. GENERAL DISCUSSION

Determination of instars of M. persicae.

It is rather difficult to distinguish some instars of M. persicae because there is perhaps no simple means on which to depend irrespective of conditions. Results of section I of this thesis show that for M. persicae reared at 15°C, 25°C and 28°C, the absolute length of the cornicle is the easiest means of distinguishing the 4 nymphal instars, and it seems possible that this absolute difference is maintained at higher and lower temperatures. But further studies need to be made to elucidate effects of environmental conditions on cornicle size.

Eastop's (unpublished) method of distinguishing the 1st instar from the 2nd by the absence of hairs on the 3rd antennal segment, although providing a correct 'identification' involves making a specially prepared mount and the use of a high power microscope, which is not always feasible for practical purposes.

The lengths of the body and of various segments depend on the quality of the food and the environmental conditions, most important of which is temperature. The size range must therefore be quite different in hot and temperate climates. In the former and where temperatures are high the insects are smallest, while in cool temperate conditions they are usually largest. The sizes of different instars therefore overlap and there is no doubt that relying on absolute lengths of characters except possibly the cornicle is erroneous if measurements are to be compared of specimens collected

in different climatic or weather conditions or from different species or quality of host plant.

Ratios between sizes of different body parts are more useful than absolute size for distinguishing different instars and this has been the basis of all methods published so far. The ratios nevertheless vary according to temperature (table 5). Futhermore at the same temperature the correlations between various parts can differ in successive generations when reared at adversely high or low temperature. (tables 25 & 26). The sizes of the different parts also do not return to normality along the same pathways of relative size changes after transfer to a favourable temperature from one where size decrease has been caused by high temperature (table 23).

Population increase.

According to the results of the present work constant temperatures lower and higher than 25°C decrease the rate of increase of the aphid population and would ultimately result in extinction at temperatures where the finite rate of increase becomes less than unity (i.e. below about 5°C or above about 30°C). But the transfer of these aphids for a period to a suitable temperature enables them to recover to a higher reproductive potential. This may help to explain how aphids can survive the conditions in the tropics and sub-tropics where temperatures are very high during the day, but relatively low during the night(according to records from the Sudan the average daily maxima for the summer ~~was~~ were about 35°C and the minima about 15°C) ; also

in temperate climates where weather is unsettled and periods of very low temperatures are followed by comparatively higher ones, or again where sunshine creates short periods of relatively high temperature even though the average temperature is harmfully low.

Experiments were done in constant temperature rooms and field populations were assessed in relation to the laboratory data; but due to the modifying effects of fluctuating temperatures in the field, the assessment of populations in this way is subject to error if the temperature limits rise above and fall below the optimum range.

Aphid samplings for two years on field populations on potatoes showed the largest number per plant to be 360. However, results of the caging experiments indicated that the number of aphids per plant in cages from which natural enemies were excluded reached about 5000 aphids. This illustrates the effectiveness of the naturally controlling factors in reducing the aphid populations in the field, and the importance of taking up a policy of integrated control. Nevertheless the rate of increase on caged potato and brussels sprout plants in the field (figs. 38 & 39), or potted plants in constant rooms (fig. 9), or on brussels sprout plants from which natural enemies were checked by insecticide plus hand picking of syrphids (fig. 42) did not approach the calculated potential rate. The possible causes of these differences were discussed before under the appropriate sections. However, among these the nutritional condition of the host plant seems to be of most importance because

the difference between the early counts on potato plants in 1968 and the calculated potential was small (fig. 36) mainly perhaps due to the rapid increase of the aphid on vigorously growing young plants.

SUMMARY

Distinguishing the various instars of Myzus persicae.

1. The sizes of different body parts of the 4 nymphal apterae were inversely related to the constant temperatures at which they were reared.

2. The mean lengths of antennae of the various instars were distinct at the same temperature, but reared at high temperatures (25°C and 28°C) the limits of lengths of the 4th instar antenna tended to overlap with those of the 3rd instar reared at a low temperature (15°C).

3. The mean lengths of the 3rd and 4th antennal segments of the 3rd instar were significantly different ($p = < 0.01$ and $p = < 0.001$) in apterae reared at 25 and 28°C, but were almost equal at 15°C i.e. the ratio between the lengths of the two segments were temperature dependent..

4. The cornicle length increased steadily from the first instar to the adult apterae, the difference between any two successive instars being significant at $p = < 0.001$. Limited data indicated that no overlapping in the limits of cornicle length occurs between the different instars irrespective of temperature but this needs confirmation.

Effects of temperature on some characters of Myzus persicae.

1. On brussels sprouts leaf-discs the nymphal developmental period decreased from 19.9 to 5.3 days with a rise in constant temperature from 10 to 29°C.

2. The 4th instar has the longest duration, the 2nd and 3rd, which are almost equal, have the shortest, and the first is about 1.1 longer than the 2nd and 3rd.

3. At 20°C nymphal developmental periods on brussels sprouts and potato leaf-discs were almost equal (7.6 and 7.8 days respectively), but at 15°C it was 1.5 days shorter on potato leaf-discs (total on potatoes = 10.3 days at 15°C).

4. The fecundity of aphids reared on brussels sprouts leaf-discs rose steadily between 10°C and 25°C, but dropped sharply at 29°C. On potato leaf-discs more young were produced at 15°C than at 20°C.

5. On brussels sprouts the fastest intrinsic rate of increase ($r = 1.8$) was calculated to occur at 25°C.

6. At 15°C and 20°C M. persicae multiplied more rapidly on potted brussels sprouts than on potato plants.

7. Transferring aphids maintained on brussels sprouts to potatoes slowed the rate of increase in numbers, while the opposite transfer had no effect.

8. The developmental period of the aphid transferred from 20°C to 27.5°C was significantly decreased in the 1st generation ($p < 0.001$). In the following generations the decrease relative to the 1st was small.

9. The developmental period of the first generation progeny of adults reared at 27.5°C for 4 and 9 generations and then transferred to 20°C was longer than of those kept constantly at 20°C. The period then decreased in successive generations and became shorter than for individuals kept constantly at 20°C.

10. The fecundity of the apterae transferred from 20°C and reared throughout at 10°C decreased to 19.4 and 5.6 in the 1st and 2nd generations respectively. Adults of F_1 and F_2 generations reared as nymphs at 10°C when transferred as adults to 20°C produced almost the same number of progeny (34).

11. Apterae reared continuously for 5 generations at a critically high temperature (27.5°C) produced 33.5, 20.8, 8.8, 5.9 and 1.8 nymphs per adult aptera in the 1st, 2nd, 3rd, 4th and 5th generations respectively. Individuals reared as nymphs at 27.5°C but kept as adults at 20°C after each generation produced 14.0, 19.8, 19.5, 22.0 and 16.8 nymphs/adult for F_1, F_2, F_3, F_4, and F_5 generations respectively. When adults of the F_4 generation reared at 27.5°C were returned to 20°C the recovery in fecundity was not complete even after 3 generations.

12. The morphometrics of the body parts of individuals transferred from 20°C to 10°C increased, while it steadily decreased in successive generations in those transferred to 27.5°C. When adults of the F_4 generation reared at 27.5°C were transferred to 20°C, it took two generations for the lengths of the different body parts to become similar to those of adults of apterae kept continuously at 20°C.

13. Correlations between lengths of various body parts were closer at 27.5°C than at 10°C; the 6th antennal segment showed the poorest correlations at both temperatures. At the 2 temperatures correlations between the lengths of the body parts were better for the F_2 generation than for the F_1 but not for later generations at 27.5°C.

Aphid populations in the field and the influence of biotic and abiotic factors.

1. Macrosiphum euphorbiae and Myzus persicae were the 2 dominant species on potatoes. Aphis nasturtii, Aulacorthum solani and Rhopalosiphonus latysiphon were either absent or scarce.

2. M. persicae and M. euphorbiae populations varied considerably from 1967 to 1968 perhaps depending on the numbers overwintering, on multiplication before immigration to potato fields, on weather conditions for flight and on multiplication within the crop.

3. M. euphorbiae mainly colonizes the upper part of the plant, and M. persicae the lower part.

4. Natural enemies seem to be more effective on potatoes in mid-summer than on brussels sprouts in autumn, because the former is frequented by more kinds of natural enemies. e.g. Coccinellids and anthocorids were virtually absent from brussels sprouts in 1967 and 1968.

5. Rain and pathogenic fungi seem to be important factors determining numbers of M. euphorbiae on the plants. M. persicae was affected more by parasites and predators. Exclusion of these natural enemies by caging or by insecticides plus hand picking of syrphid eggs resulted in rapid increase in aphid numbers.

6. The main aphidophagous insects seen on brussels sprouts were the parasites and syrphids, but the latter had negligible effect in controlling aphid increase. Less known insect predators e.g.

staphylinids, carabids and nabids may be very important in checking M. persicae numbers on brussels sprouts.

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Mrs M. van Emden for translating German papers.

Mrs J.Minett for typing this thesis.

Mr. H.O.Devitt for the photographic work.

All Field Station personnel who helped in many ways.

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